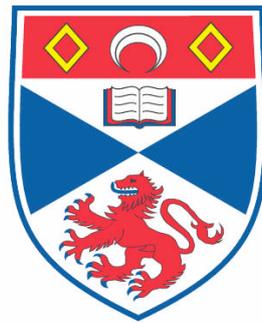


Chimpanzee (*Pan troglodytes*) Gaze Following in the
Informed Forager Paradigm: Analysis with Cross Correlations

Katherine McGregor Hall



This thesis is submitted in partial fulfilment for the degree of PhD
at the
University of St Andrews

December 15, 2011

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Abstract

I tested two pairs of captive chimpanzees (*Pan troglodytes*) in the informed forager paradigm: a subordinate saw the location of hidden bait, and then searched with a naïve dominant. This paradigm has tested what subjects know about others' states of knowledge, but my focus was to determine *how* subjects used different movement types and different gaze types to modify their competitive tactics.

In particular, I investigated whether chimpanzees follow opponents' gaze to gain information. Learning more about how primates use visual information to predict others' behaviour can shed light on the continuing debate over to what degree apes possess theory of mind capacities.

Previous published studies in this paradigm included narratives of ignorant competitors exploiting informed subjects by following their movement and gaze, and informed subjects avoided this exploitation by walking away from hidden food. The subordinate's behaviour can be considered tactical deception, which is a good place to seek strong evidence of second-order intentionality.

Analyses with descriptive statistics, however, fail to capture the complexity of these interactions, which range from single decision-making points to larger patterns of following and misleading. I introduced a novel method of statistical analysis, cross correlations, that enabled me to examine behavioural patterns quantitatively that previous authors have only been able to describe in narrative form.

Though previous studies on chimpanzees' understanding of gaze found that they were unable to use (human-given) gaze cues to locate hidden food, the subjects I tested followed their conspecific opponent's gaze, and used information gained from the gaze interaction to modify their own movement towards the hidden bait. Dominants adjusted their physical following of the subordinates as the interaction progressed, which reflected their changed states of knowledge. Subordinates used their movement and gaze differentially to manipulate dominants' behaviour, by withholding information and by recruiting towards a less-preferred bait.

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I. Background of problem

In 1974, Emil Menzel created a novel experimental paradigm to study information transfer within a group of animals, and presented his results from using the design with a group of young chimpanzees. His work, and the many subsequent replications and extensions, have raised many questions about what chimpanzees understand about what others know, how they gain information from social partners in a foraging situation, and how they manipulate opponents through tactical deception. In this “informed forager paradigm,” a subordinate individual is shown the location of a hidden food item, and then released into an arena to search with an ignorant dominant competitor (Menzel, 1974). The dominant can easily exploit the foraging success of the subordinate through physical or social pressure (Baker et al., 1981; Rohwer & Ewald, 1981; Barta & Giraldeau, 1998); thus the subordinate has a high incentive to behave in a way that prevents the dominant from finding the food.

In particular, Menzel’s narrative of the competition between two chimpanzees, Belle and Rock, was one of the starting points for investigating more about tactical deception and second-order intentionality in primates (Byrne & Whiten, 1988, 1990). Menzel wrote:

“If tested when Rock was not present, Belle invariably led the group to food and nearly everybody got some. In tests conducted when Rock was present, however, Belle became increasingly slower in her approach to the food. The reason was not hard to detect. As soon as Belle uncovered the food, Rock raced over, kicked or bit her, and took it all.

Belle accordingly stopped uncovering the food if Rock was close. She sat on it until Rock left. Rock, however, soon learned this, and when she sat in one place for more than a few seconds, he came over, shoved her aside, searched her sitting place, and got the food.

Belle next stopped going all the way. Rock, however, countered by steadily expanding the area of his search through the grass near where Belle had sat.

Eventually Belle sat farther and farther away, waiting until Rock looked in the opposite direction before she moved toward the food at all—and Rock in turn seemed to look away until Belle started to move somewhere. On some occasions Rock started to wander off, only to wheel around suddenly precisely as Belle was about to uncover the food.

Often Rock found even carefully hidden food that was 30 ft or more from Belle, as he oriented repeatedly at Belle and adjusted his place of search appropriately if she showed any signs of moving or orienting in a given direction. If Rock got very close to the food, Belle invariably gave the game away by a ‘nervous’ increase in movement. However, on a few trials she actually started off a trial by leading the group in the opposite direction from food, and then, while Rock was engaged in his search, she doubled back rapidly and got some food. In other trials when we hid an extra piece of food about 10 ft away from the large pile, Belle led Rock to the single piece, and while he took it she raced for the pile. When Rock started to ignore the

single piece of food to keep his watch on Belle, Belle had temper ‘tantrums’” (Menzel, 1974, p.134-135).

These interactions indicate that each chimpanzee was aware of what the other wanted—to find the food—and that they understood the effects of employing their tactics and counter-tactics: Rock’s actions were to gain information from Belle in order to take the food, and Belle’s actions were to prevent Rock from finding it. They both acted with the intention to achieve the goal of the food reward, and flexibly reacted to their partner’s behaviour in ways that have been interpreted to indicate second-order intentionality in their deceptive behaviour (Byrne & Whiten, 1990).

II. Statement of problem

Stories such as the one of Belle and Rock have been regarded as anecdotes in the pejorative sense, though they should rather be considered records collected by experienced observers of unique behaviour, that serve as a starting point for more research (Whiten & Byrne, 1988; Byrne, 1997; McGrew, 2004; Sarringhaus et al., 2005). Menzel’s narrative in particular has motivated several follow-up studies that have attempted to address tactical deception in the subjects, and what each subject may know about the other’s state of knowledge (Coussi-Korbel, 1994; Held et al., 2000, 2002, 2010; Hare et al., 2001, 2003; Hirata & Matsuzawa, 2001; Ducoing & Thierry, 2003, 2004; Bugnyar & Kotrschal, 2004; Schloegl et al., 2008b).

The question of whether chimpanzees reason about the knowledge of others has ignited a debate over chimpanzees’ theory of mind capacities (Premack & Woodruff, 1978; Heyes, 1998). Specifically, many studies have focused on one particular aspect of theory of mind: chimpanzees’ understanding of attention as a mental state (Povinelli & Eddy, 1996; Reaux et al., 1999; Kaminski et al., 2004; Bulloch et al., 2008). However, a general problem with these studies is that the chimpanzee subjects are required to demonstrate their understanding of a human experimenter’s gaze as indicating the location of a bait hidden under one of two opaque cups. Chimpanzees may not understand the significance of a human’s gaze, or the significance of a visual communicative signal given by a human (Gómez, 1996; Matheson et al., 1998; Hare & Tomasello, 2004). Moreover, chimpanzees may not understand the role of eyes in attention at all, due to their own dark pigmented sclera

(Povinelli & Eddy, 1996a; Kobayashi & Kohshima, 2001; Tomasello et al., 2007). Many object choice or begging paradigm studies are not ecologically valid for these three reasons.

Though several additional records of deception in settings of competition among conspecifics have been collected and published, analyses have usually failed to show statistically the interactions that observers described as happening. For example, a report of the mean percentage of food items that either competitor obtained does not describe the interaction that led to that outcome; stating whether the competitors could see each other at the time of baiting reveals nothing interesting about how either individual used visual information to modify their own competitive tactic. There has been a frustrating lack of detail in the statistics used to substantiate claims of tactical deception.

All previous work on chimpanzee gaze understanding has either tested subjects in some one-shot task without consideration of ecological validity, or has concentrated entirely on the question of *what* chimpanzees understand, ignoring the equally important question of *how* chimpanzees use visual information in more realistic competitive interactions. In particular, there is a lack of an appropriate statistic to handle data on gaze interactions. There is therefore an empty niche for me to investigate how competing chimpanzees interact, so as to analyse familiar data (that stemmed from the original study by Menzel) in a novel way.

III. Purpose of study

Researchers have studied the link between gaze following and knowledge attribution in chimpanzees—questioning whether chimpanzees have mental states, attribute mental states to others, and what the content of those mental states would look like. Yet clear experimental evidence of chimpanzee mental state understanding eludes the field. My work specifically focuses on gaze following as evidence that chimpanzees are trying to gain information from a conspecific. In this way, I approach the question of *how* chimpanzees gain knowledge, rather than *what* is the content of their knowledge (i.e. what they are mentally representing). I ask questions such as, “How does a chimpanzee gain knowledge from another?” and “How does a chimpanzee use that information to alter her own behaviour?”

The purpose of this dissertation is to adapt a statistical method capable of capturing the complexity of the interactions between subjects, from single decision-making points to larger patterns of withholding and misleading. With the help of Dr. Mike Oram, I have

adapted a statistical method from neurology, *cross correlations*, for use in analysing animal behaviour, in order to show the behavioural contingencies that exist between two individuals over time (Aertsen et al., 1989). Rather than using a contrived experimental situation—or worse, a human demonstrator—to address the questions of knowledge and ignorance, I have returned to the original paradigm in which these questions were first raised: the informed forager paradigm.

IV. Outline and Research questions

This dissertation summarises previous research in the field on topics related to primate social intelligence, gaze understanding, the informed forager paradigm, and tactical deception, in Chapter 2: Literature Review. Chapter 3: Experimental Methods describes how I carried out two experiments, *Competition* and *Unequal Rewards*. In Chapter 4: Statistical Methods, I review how previous studies in the informed forager paradigm have presented their analyses, point out their shortcomings in providing the level of detail desired to show the interesting behaviour that the authors describe, and develop an adaptation of cross correlations for use with my study. I use cross correlation analyses in Chapters 5-7 to address several research questions. I focus on specific details of the subjects' movement (Chapter 5) and gaze (Chapter 6), and their use of different gaze tactics (Chapter 7) so as to approach answers to larger questions such as those posed below. In Chapter 8: Discussion, I summarise the findings of my research and discuss their implications. This dissertation adds to the scientific discussion of three important questions, outlined below.

A. Does the dominant know that the subordinate knows where the food is, and act to exploit that knowledge?

My focus is not *what* one subject knows about another's knowledge; I can only observe behaviour and statistically demonstrate how each subject's behaviour changes over the course of the experiment. In previous informed forager studies, researchers described the ignorant dominant as giving the impression that she was aware that the subordinate had privileged information, by following in order to take food once the subordinate uncovered it. To answer the question posed here, "does the dominant know that the subordinate knows where the food is, and act to exploit that knowledge?," I focused on a micro-analysis of each subject's movement within their enclosure, relative to the hidden bait and relative to each other (see Chapter 5: Movement Following). As a singular definition was inadequate to

portray the variety of behaviour observed (Leca et al., 2003; Meunier et al., 2008; Sueur & Petit, 2008, 2010; though see Stueckle & Zinner, 2008, for “leading from the back”), I defined three types of movement following: follow by *approaching*; follow in the other’s *footsteps*; and follow by *converging* on the other’s destination. The dominants (naïve to the experimental situation) did not follow their subordinate opponents at the beginning of the experiment; they only learned over several trials to do so. The *change* in their behaviour suggests that they came to know that the subordinates knew where to search. By following the subordinates, the dominants were able to gain knowledge about where the food was hidden, and to exploit by taking it, or by walking ahead of the subordinate’s path to search.

I continued to explore how the dominant gained knowledge using visual cues (See Chapter 6: Gaze Following). I defined two types: *static* gaze following, and following gaze *onset*. Contrary to predictions extended from Chance’s (1967) social attention hypothesis, dominants followed the subordinates’ gaze using both types more than the reverse. Furthermore, dominants used information gained from following subordinates’ gaze to adjust their movement while following.

B. Does the subordinate act to avoid the dominant’s exploitation?

In Chapter 5 I also describe changes in subordinates’ movement in the enclosure. In previous informed forager studies, the informed subordinate was described as occasionally delaying approach to the food, which functioned to withhold information from the dominant, or taking an indirect route to the food, which functioned to mislead the dominant. To answer the question posed here, “Does the subordinate act to avoid the dominant’s exploitation?,” I focused on the contingency between the dominants’ following behaviour and the subordinates’ subsequent behaviour. In the later stages of the experiment, when the dominant exerted exploitation pressure by following closely, subordinates tended to delay their approach to the food. I showed that when subordinates paused their movement, they were also likely to stop gazing towards the location of the hidden bait (see Chapter 6). This functioned to withhold visual information from dominant competitors, and can be classified as tactical deception. The subordinates acted intentionally to prevent the dominants from getting closer to the bait by delaying their own approach to the food, and by gazing in a different direction, thus acting to achieve their ultimate goal of obtaining the hidden food reward.

C. In the presence of a less valuable reward, does the subordinate lead the dominant to the decoy?

Researchers have previously described informed subordinates as searching for food in empty containers or first approaching hiding places with less food; since they had learned that dominant competitors would follow, the subordinates allowed the dominants to take food from the smaller pile while the subordinates turned around to retrieve the larger reward. To answer the question posed here, “In the presence of a less valuable reward, does the subordinate lead the dominant to the decoy?” I focused on the outcomes of interactions between competitors over a banana and a cucumber, as well as a micro-analysis of the subordinate’s use of two different types of gaze tactic: *monitoring*, and *recruitment*, leading up to those outcomes (see Chapter 7). Subordinates used *monitoring* glances only before approaching the banana, but *monitored* throughout their approach to the cucumber. Additionally, subordinates *recruited* towards the cucumber but not the banana, suggesting that they flexibly used the tactic of pausing and alternating gaze between the dominant opponents and the cucumber bait to intentionally attract the dominants to approach.

V. Importance of study

A. Ecologically valid experimental study

By returning to the original informed forager paradigm, my subjects did not need to understand a human demonstrator’s gaze, or a cooperative cue; it was possible to observe chimpanzees behaving in a naturalistic food competition scenario with a conspecific, as they do on a daily basis. Though Hare et al. (2000, 2001) conducted competitive experiments with conspecifics, the experimental setup was very artificial. Subjects had only a few seconds and a few metres of space to decide whether to approach a food item as their doors were opened into the competition cage—hardly enough time or space to fully develop a competitive strategy, much less a deceptive tactic where appropriate. In my study, subjects had the full space of their outdoor enclosure and up to five minutes to retrieve the hidden food (subjects never needed more than the time allotted).

B. Addresses gaze following as source of information gain

Previous studies in the object choice paradigm have shown that chimpanzees generally fail to use visual cues to gain information about another individual’s knowledge

regarding a hidden food item (Povinelli & Eddy, 1996; Reaux et al., 1999; Bulloch et al., 2008). However, due to methodological challenges (Hare & Tomasello, 2004) and perhaps problems with the type of analysis (Ruiz et al., 2008), the results from these studies are not definitive. My study provides detailed evidence that chimpanzees follow conspecific gaze in a naturalistic foraging scenario, and the strongest experimental evidence thus far that they use visual information to modify their competitive tactics.

C. Presents new statistical method to describe detailed contingent interactions

Using the cross correlation analysis provides the most detailed and most comprehensive look at how chimpanzees use “continuous feedback” (Menzel, 1974, p. 134) when monitoring their competitor’s behaviour. This method validates previous studies, but in a more sophisticated way. Cross correlations show changes over time in an individual’s behaviour, and show that one individual’s behaviour is often contingent on her opponent’s. Therefore, this statistical method can demonstrate a relationship that other authors have indicated seems to exist, but which their analyses did not conclusively show (or, it can elucidate relationships where none were thought to exist, and where one might not have thought to look).

Two different noise distributions were computed by randomly permuting the data from the experiments themselves, and then the original data were compared to these noise distributions to test particular hypotheses. This allowed me to create a baseline where none previously existed. This baseline is the theoretical distribution of the probability of a relationship appearing by chance. Comparing the dataset to the shuffled baselines using *t*-tests and $-\log$ -likelihood values indicates statistical significance, and one baseline can be preferred to the other depending on the question being asked.

VI. Summary

My dissertation work provides a detailed analysis of chimpanzee movement-following and gaze-following in the informed forager paradigm. Its scientific merit lies in the development of the cross correlation statistic for use in analysing animal behaviour: cross correlations can show the timing of contingencies that exist between competing foragers, as well as how their behaviour changes over time. The resulting correlogram is a new graphical representation of data that are already familiar from narrative description of competitors’ interactions. Furthermore, using this method has allowed me to bring to light a result that has

long been described but not properly analysed, that of chimpanzees using gaze following to gain information from others, information which is in turn used to modify their own competitive tactics.

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I. Abstract

Primates act intentionally to achieve goals, often through social manipulation. Each agent in an interaction can behave flexibly in response to others' actions, and an agent can outwit others by predicting their behaviour. The question of whether mental representations or thoughts, rather than solely instinctive tendencies and learning, underlie behaviour introduces the debate over theory of mind: the ability to attribute to others mental states such as desires, thoughts, intentions and beliefs. Do chimpanzees interact with each other as they do because they reason about others' mental states, and believe that these mental states cause behaviour? Does mental state attribution play a role in deceptive interactions? An important question is which skills or abilities might provide evidence that a subject attributes or infers a mental state of another individual. One skill that may facilitate researchers' ability to detect the attribution of attention and knowledge to others is a chimpanzees' ability to understand and interpret another's gaze, particularly aspects of gaze following and visual perspective taking. Many experiments have been carried out with chimpanzees to test the hypothesis that the physical act of seeing leads to the mental state of knowing, and the pattern of positive results speaks to the importance of ecological validity in experimental design. Further investigation has shown that when chimpanzees attempt to follow the gaze of another, they may consider the other's head orientation to be a more salient cue than their eye direction. It has been suggested that humans' white sclera (without pigment), as well as aspects of gaze behaviour, evolved in the context of cooperative interactions. Chimpanzees are indeed more obviously competitive than humans, and like other species of primate they develop alternative strategies to cope with the pressures of competitive social life by engaging in tactical deception. The informed forager paradigm has been elaborated to investigate different deceptive strategies used in a competitive situation.

II. Psychological Agents

A. Primate Social Intelligence

Given the biological and behavioural continuity of non-human primates (hereafter primates) and human primates (hereafter humans), there is reason as well to hope for the prospect of a cognitive continuity between these two groups. Primates' cognitive abilities have evolved to flexibly cope with the complex social interactions that take place between group members. Primates are exceptional at social manoeuvring, and many theories that

attempt to explain primate intelligence centre on the tenet that increased social group size requires an increase in behavioural repertoire to cope with the challenges of social living (Chance & Mead, 1953; Humphrey, 1976; Jolly, 1966; Kummer, 1967; Byrne & Whiten, 1988; Whiten & Byrne, 1997; Dunbar, 1998). Humphrey (1976) emphasises the flexible framework of social interactions:

“One animal may, for instance, wish by his own behaviour to change the behaviour of another; but since the second animal is himself reactive and intelligent the interaction soon becomes a two-way argument where each ‘player’ must be ready to change his tactics—and maybe his goals—as the game proceeds” (Humphrey, 1976, p. 307).

This is the essence of *Machiavellian Intelligence*: that each actor in a social interaction must flexibly adapt his or her behaviour as the interaction evolves (Byrne, 1996), either manipulating another for personal gain (Wilson et al., 1996), or during cooperation to maximize one’s own fitness (Byrne, 1996). The problem of prediction arises: there is a functional advantage to being able to out-manoeuvre one’s competitors by anticipating their future behaviour (Whiten & Byrne, 1988).

In order to predict others’ future behaviour, humans can attribute mental states to others such as desires, thoughts, knowledge, and beliefs; this ability is known as Theory of Mind (Premack & Woodruff, 1978; Baron-Cohen, 1995). Humans conceive of the ‘self’ as an agent that recognizes it’s own desires and thoughts (Whiten & Perner, 1991), and acts upon them intentionally (Astington & Gopnik, 1991). We believe that others, like ourselves, have the same abilities, and we attribute these abilities to them. A framework in which one assumes that everyone mentally represents situations in the same manner as oneself allows for the possibility for one to infer another individual’s mental state, and then predict their behaviour (Dennett, 1971, 1987; Leslie, 1991; Baron-Cohen, 1995). In research on mental state attribution in primates, however, there is the obvious problem for the ethologist: to decide whether an animal’s behaviour was intended to change another individual’s behaviour, or their thoughts (indeed, whether it was intended at all, or simply instinctual). Many studies have instead focused on whether it is essential to use mental state attribution in an explanation of primate behaviour (Premack & Woodruff, 1978; Cheney & Seyfarth, 1990; Povinelli & Eddy, 1996; Hare et al., 2000, 2001).

B. Behaviour-reading versus Mind-reading

Humans often treat animals as if they are intentional beings with their own set of desires and thoughts about the world; sometimes this stretches into anthropomorphism, or the attribution of human characteristics to animals. Many early psychologists published anecdotes and experiments on animal behaviour and attributed to their subjects qualities such as intentions, desires, and thoughts (Romanes, 1883; Köhler, 1925; Griffin, 1978). However, because these mental states are not objectively observable phenomena, there is an argument against treating animals as having them, on the basis of parsimony, and instead for rigorously describing their visible past behaviour with the aim of predicting their subsequent behaviour (Skinner, 1984; Bennett, 1991; Heyes, 1987; 1998). This strict behaviouristic approach sponsors the attitude that anecdotes of behaviour described in ‘mentalist’ terms cannot be taken seriously in a scientific realm (Morgan, 1894; Whitman, 1899; Skinner, 1984). Moreover, while anecdotes provide accounts of unique behaviour, they are considered at best a starting point for more rigorous explanation (Whiten & Byrne, 1988; Byrne, 1997; McGrew, 2004; Sarringhaus et al., 2005).

Underlying the argument over whether to use mentalistic terms to describe behaviour is the more fundamental question of whether the animals in question experience their lives in an intentional framework (Byrne & Whiten, 1991; Gómez, 1991, 2005): do animals interact with each other as they do because they reason about others’ mental states, and believe that these mental states cause behaviour (mind-reading)? Or do animals simply make associations about others’ behaviour and likely outcomes, based on previous experiences, in order to predict their future actions (behaviour-reading)? The debate centres on whether animals act as behaviour-readers, or mind-readers, and whether human observers are able to collect behavioural evidence that would differentiate between the two theories, as evidence for mind-reading appears the same as evidence for behaviour-reading. Whiten (1996) points out that the recognition of another’s state of mind must be based on observations of others’ behavioural patterns, as well as the environmental context of said behaviour. I agree, and throughout this dissertation I treat chimpanzees as psychological agents that perceive goals and behave intentionally, flexibly and appropriately to achieve them, especially through social manipulation (de Waal, 1982). Experimental evidence of mental state representation, as decoupled from, and the ultimate cause of behavioural manifestation (Gómez, 2009),

eludes the field. My work focuses more on *how* chimpanzees gain knowledge from conspecifics, rather than *what* they know, i.e., the content of their mental states.

As Bennett (1978) and Premack and Woodruff (1978) argue, adopting the intentional stance while describing behaviour, i.e., assuming rationality in another being (Dennett, 1971, 1987), not only shortens the explanation of a particular behaviour, but also efficiently frames it in a vocabulary with which all readers are naturally familiar and understand. Heyes (1998), however, reasons that explaining animal behaviour using mentalistic descriptions and psychological representations might not be justified simply because they are easiest for us as readers to understand; a behaviouristic explanation may be more appropriate. Furthermore, Penn and Povinelli (2007) argue for showing the causal necessity of mental states in addition to, and distinct from, cognition without them (see also Povinelli & Vonk, 2003). Byrne and Bates (2006) argue that the parsimony of describing how an animal learns to make associations between events quickly becomes overly complicated when trying to describe real-life scenarios; additionally, post-hoc explanations of this type are not predictive of future behaviour. I advocate Byrne and Bates' cognitive explanation, to develop theories with testable predictions that can be mapped onto observable behaviour. Premack (1988a) suggested that if non-humans make mental attributions, they may be limited to a subset of what a human can attribute (Call & Tomasello, 2008). For example, non-humans may not be able to produce multiply embedded attributions such as 'Sue thought that Hillary wanted Jeff to believe that X,' something that most humans can do by four years of age (Wimmer & Perner, 1983; Dennett, 1988b).

C. Theory of Mind

Premack and Woodruff (1978) experimentally approached the question of whether animals attribute mental states to others, and defined this phenomenon as Theory of Mind:

"In saying that an individual has a theory of mind, we mean that the individual imputes mental states to himself and to others (either to conspecifics or to other species as well). A system of inferences of this kind is properly viewed as a theory, first, because such states are not directly observable, and second, because the system can be used to make predictions, specifically about the behaviour of other organisms" (Premack & Woodruff, 1987, p. 515).

This definition raises questions as to whether thoughts precede action, and if understanding another's thoughts can aid in predicting their actions.

1. Do primates reason about others' mental states?

Premack and Woodruff (1978) presented their chimpanzee subject, Sarah, with a series of video clips in which a human actor faced a problem, such as reaching for an inaccessible item, or trying to light a heater, and then gave her a choice between two photographs, one depicting the solution to the problem. Unrewarded, the chimpanzee correctly chose the solution photo, and the authors initially interpreted the results as evidence that chimpanzees could make attributions: Sarah understood the video not as a sequence of events but as the depiction of a problem. Therefore, the solutions she chose were correct because she attributed to the actor the intention to solve the problems, as well as the knowledge of how to solve them. However, Premack and Woodruff's article was criticized in the commentaries, which claimed that Sarah's behaviour represented simple learning of relationships between objects, rather than evidence of mental state attributions including intention and knowledge. Premack and Woodruff noted that Sarah's understanding of the problems faced by the actor in the video was based on observational learning, but argued that this familiarity was not enough to explain Sarah's correct predictions of the actor's future behaviour. Premack (1983, 1988) later re-evaluated Sarah's performance on his experiments and proposed that chimpanzees may attribute intention, but not attribution itself (second-order attribution, i.e., Sarah's beliefs about the actor's intentions).

2. Components of Theory of Mind

After multiple researchers had published studies on the topic of mental state attribution (see review below), following Premack's (1983) revision, without anyone coming to a definitive answer to the question 'do animals have it?', Hare et al. (2001) reminded colleagues that rather than focus on the big-picture question, researchers should dedicate efforts to studying "a whole panoply of more nuanced questions concerning precisely what chimpanzees do and do not know about the psychological functioning of others" (p. 149). That is to say that theory of mind is not a single entity but rather a collection of abilities ranging from self-recognition (Gallup, 1970), understanding social relationships (Cheney & Seyfarth, 1990a), and visual perspective taking (Tomasello, et al., 1999), to imitation (Tomasello, 1996; Whiten, 1996a,b), role taking (Povinelli et al., 1992a) and deception (Whiten & Byrne, 1988; Cheney & Seyfarth, 1991). Most primates have at least some components of Theory of Mind.

III. Social Attention

A. Types of Gaze

Emery (2000) distinguishes the types of social gaze (Figure 2.1). When two individuals direct their attention to each other, they engage in *mutual gaze*. If only one partner directs his attention to the other (but gaze is not mutual), this is called *averted gaze*. *Gaze following* occurs when one individual notices that another is looking to a point in space, and follows the other's line of sight to that point. When an object or other focus of attention is present at that point, the two individuals have *joint attention* on that object. *Shared attention* combines mutual and joint attention, in that both individuals are aware that the other is also looking at the same object as oneself. Theory of mind unites all of the aforementioned types of social gaze with higher-order cognition so that both individuals can attribute to the other thoughts, beliefs, or intentions towards the object.

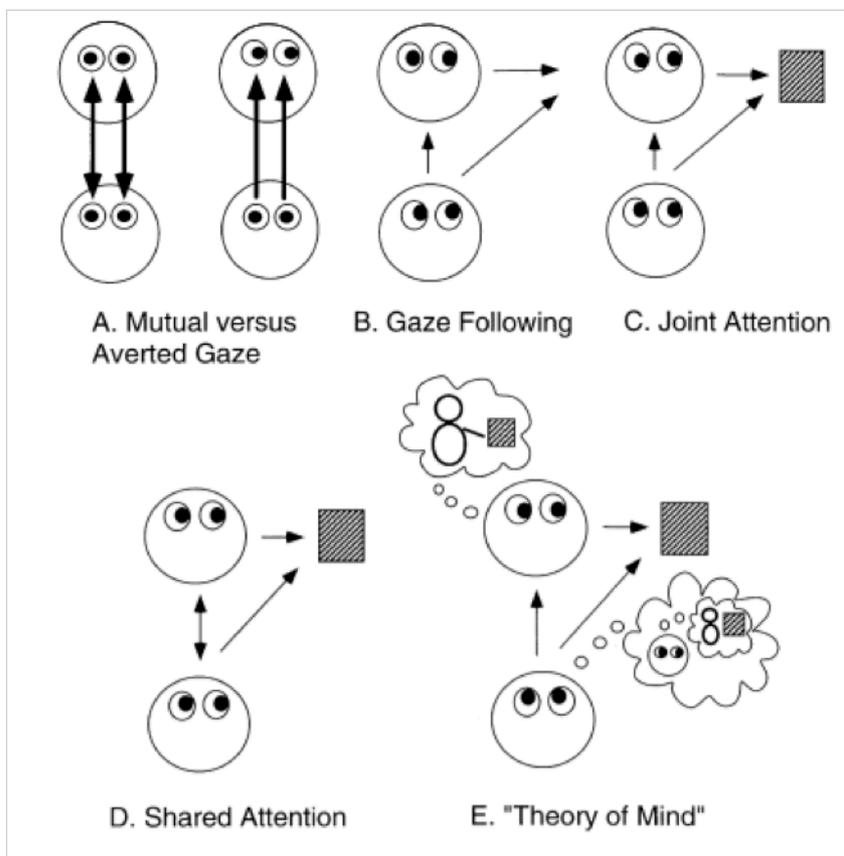


FIGURE 2.1: Types of social gaze (taken with permission from Emery, 2000, and edited to fit the page)

Episodes of joint attention (such as a human demonstrator and chimpanzee subject both looking at a baited cup) have often been the subject of debate over whether participants understand another's attention as a mental state rather than a physical or behavioural property. Gómez (1998) argues that to perceive attention, which is not a physical entity, does not necessitate inferring another's mental state (though apes do understand attention as intersubjective, which is different from their understanding of physical objects, as evidenced by their attention-calling and attention-checking behaviours: see Gómez, 1998; Hostetter et al., 2007).

B. Gaze Following in Primates and Others

It has been established that many primate species follow the gaze of their conspecifics and/or human experimenters, from prosimians such as ring-tailed lemurs (*Lemur catta*) (Shepherd & Platt, 2008), common brown lemurs (*Eulemur fulvus fulvus*) and black lemurs (*E. macaco macaco*) (Ruiz et al., 2008), to Old World monkeys such as Diana monkeys (*Cercopithecus diana diana*) (Scerif et al., 2004), sooty mangabeys (*Cercocebus atys torquatus*), stumptail macaques (*Macaca arctoides*), pigtail macaques (*M. nemestrina*) (Tomasello et al., 1998), rhesus macaques (*M. mulatta*) (Emery et al., 1997; Tomasello et al., 1998), New World monkeys including common marmosets (*Callithrix jacchus*), cotton-top tamarins (*Saguinus oedipus*), capuchins (*Cebus apella*), and squirrel monkeys (*Saimiri sciureus*) (Neiworth et al., 2002; Anderson et al., 2005; Burkart & Heschl, 2007), and all great apes (*Gorilla spp.*, *Pongo spp.*, *Pan spp.*) (Tomasello et al., 1998; Bräuer et al., 2005, Okamoto-Barth et al., 2007).

Many non-primate species have been found to follow gaze as well, suggesting that the ability is widespread throughout the animal kingdom, especially in highly social species: domestic dogs (*Canis familiaris*) (Hare & Tomasello, 1999), common ravens (*Corvus corax*) (Bugnyar et al., 2004; Schloegl et al., 2007), Northern bald ibises (*Geronticus eremita*) (Loretto et al., 2010), horses (*Equus caballus*) (McKinley & Sambrook, 2004), domestic goats (*Capra hircus*) (Kaminski et al., 2005), wolves (*Canis lupus*) (Range & Virányi, 2011), and even in some solitary species such as the red-footed tortoise (*Geochelone carbonaria*) (Wilkinson et al., 2010).

C. Understanding Gaze Following

During social interactions, humans can understand the visual perspective of others (Butterworth & Jarrett, 1991), can manipulate the attention of others with both gestures and

deictic gaze (Gómez, 1996; Shepherd, 2010) and can often infer another person's mental state through this understanding (Baron-Cohen, 1991). Gaze following—noticing another individual's direction of attention to a point in space and then adjusting one's own line of regard to the same point in space (Emery, 2000)—is generally recognized as a key precursor to full (human-like) theory of mind, because it is a process by which one can gain information about another individual's attention (Baron-Cohen, 1991; Gómez, 1991; Whiten & Byrne, 1991; Whiten, 1997; Emery, 2000; Bulloch et al., 2008; Zuberbühler, 2008). The ability to follow gaze is important for gaining information from group-mates about the social hierarchy (Chance, 1967; McNelis & Boatright-Horowitz, 1998; Kaplan & Rogers, 2002; Shepherd et al., 2006), about the location of food or predators (Hare et al., 2000; Schloegl et al., 2007; Zuberbühler, 2008; Rosati & Hare, 2009), and during observational learning (Emery et al., 1997). Gaze following is also necessary in visual perspective taking, for example geometric gaze following around barriers in order to see what another sees hidden behind an obstruction (Tomasello et al., 1999; Bugnyar et al., 2004; Shillito et al., 2005; Loretto et al., 2010). Furthermore, gaze following may play a role in deception: one's unconscious eye movements may leak information to others about the truth (Freire et al., 2004). Importantly, there is a connection between the overt behavioural act of seeing and the mental state of knowing: one who witnesses an event has knowledge about it (Wimmer et al., 1988; Povinelli et al., 1999; Hare et al., 2001). Thus, learning more about how primates use and understand others' visual perspective, and use visual information to predict others' behaviour, can shed light on the continuing debate over to what degree apes possess theory of mind capacities.

IV. Review of Chimpanzee Gaze Understanding

A. Can Chimpanzees Attribute “Attention”?

Call et al. (1998) demonstrated that chimpanzees follow a human experimenter's gaze. In their study, a human gazed with both head and eye orientation to a location above the chimpanzee subject, on the ceiling of the subject's cage; in control trials, the experimenter simply stared at the chimpanzee subject for ten seconds. Subjects looked up to the ceiling more in the gaze condition than during the control, showing their ability to follow a human's gaze. The authors note that upon following the human's gaze to the ceiling where nothing interesting was found, the subjects 'checked back' to the face of the experimenter,

and sometimes again to the ceiling. It may be the case that chimpanzees understand the purpose of gaze and that when they fail to gain interesting or unusual information, check back to the gazer's face for further information. An alternative explanation posits that chimpanzees expect some behaviour from the experimenter, for example a food reward, and look back to his face in anticipation. It is also possible that the subjects' multiple gazes to the ceiling are independent events: they follow the human's gaze, see nothing, return to neutral, and follow the human's gaze to the ceiling again; in this explanation, the gazes are not motivated by understanding. However, given that checking-back behaviour has been described in primates in numerous situations including gestural communication (Tomasello et al., 1994), social referencing (Russell et al., 1997), and joint attention (Carpenter et al., 1995; Scerif et al., 2004; Ruiz et al., 2008), this mechanistic explanation seems unlikely.

Following the work of Call et al. (1998), many studies have been conducted to determine whether chimpanzees are capable of attributing the mental state of attention to a person who has open eyes. For example, chimpanzees should beg for food more from a human that is looking directly at them, versus one that is turned away or has closed eyes (see Flombaum & Santos, 2005 for an alternative version of this paradigm). Povinelli et al. (1996), Reaux et al. (1999), Kaminski et al. (2004), and Bulloch et al. (2008) tested chimpanzees for their understanding of human demonstrators' attention with varying manipulations of the visual access that each experimenter had, using a variety of props and postural cues. For example, experimenters covered their eyes with buckets over their heads, blindfolds, handheld screens, and sat with their faces uncovered but looking away from the subject, or sat with their backs towards the chimpanzee subjects. The correct experimenter for the chimpanzee to beg from was always the person looking at the subject with direct eye contact. Povinelli et al. (1990) and Reaux et al. (1999) noted that in some conditions the chimpanzees could have successfully begged from the correct experimenter by learning simple rules such as *choose the person whose face I can see*. Often, the more basic rule, *choose the person with frontal orientation*, took precedence over the most advanced rule, *choose the person with open eyes*. In fact when given the choice between a person facing away but looking back over her shoulder, and a person facing forwards with eyes closed, the chimpanzees significantly preferred the incorrect option, that of the person facing forward with closed eyes (Reaux et al. 1999). However, Bulloch et al. (2008) found evidence contrary to Reaux's proposition that chimpanzees learn associative rules: Bulloch argued that

‘enculturated’ chimpanzees had enhanced understanding of human visual attention, and performed successfully from the beginning of the experiment. Ultimately, the enculturated chimpanzees also failed in the look-over-the-shoulder condition, and could not inhibit their choice of a person with a frontal posture. Kaminski et al. (2004) suggested that chimpanzees’ choice to beg from a person with frontal posture indicated their perception of the human’s predisposition to hand over food compared to someone facing away. Subjects may have begged from a human with frontal body orientation as a ‘safe’ begging strategy, though it is not sophisticated in terms of their understanding the importance of the eyes as indicative of an attentive state. Kaminski further argued that chimpanzees may still understand *seeing* in others in most cases from a general sensitivity to the face as a whole, rather than the eyes alone.

B. Can Chimpanzees Attribute “Knowledge”?

A related research question is whether chimpanzees can attribute knowledge of a scene to a person that has seen it. For example, if subjects can make the connection that an experimenter who has observed an important event, such as baiting a food reward in an opaque container, has gained knowledge from witnessing the event, then they should be able to modify their begging behaviour to target the experimenter that had witnessed the baiting (the ‘knower’), rather than one that had not (the ‘guesser’). This is the essence of the guesser-knower object choice paradigm (Anderson et al., 1995; Call et al., 1998; Itakura et al., 1999; Povinelli et al., 1999; Call et al., 2000; Vick & Anderson, 2000; Hare & Tomasello, 2004; Barth et al., 2005; Brauer et al., 2006; Bugnyar, 2007; Schloegl et al., 2008a,b; Bugnyar, 2011). In these studies, human experimenters provided different communicative cues to the subjects to indicate the location of a hidden food item under one of two cups, such as tapping, pointing, head orientation and gaze, and eye direction alone. While the various studies reported that subjects preferred begging from the ‘knower,’ they indicated that overall, for a subject to choose the correct experimenter, head orientation was a much stronger cue than only the eyes gazing towards the baited cup (Povinelli & Eddy, 1996; Povinelli et al., 1999; Vick & Anderson, 2000; similar tests with other gaze-following species such as ravens show that they do not use experimenter or conspecific gaze cues to find a hidden bait, Bugnyar, 2007; Schloegl et al., 2008a,b). Similar to previous studies, subjects could have chosen the correct experimenter based on learning simple rules related to body/head/eye orientation, e.g., *avoid experimenters with buckets over their heads*; they did not necessarily need to

understand the experimenters' knowledge states as a product of having seen where the food was hidden.

While chimpanzees do not seem to understand human gaze as indicating the location of a hidden food, perhaps analysing the data differently may reveal that they do. Ruiz et al. (2008) propose 'gaze priming' as a way to understand choices that two lemur subject species made in an object choice task: though choices appeared random, upon closer inspection it was found that when a subject followed a model's gaze, they were more likely to choose the correct food container.

Heyes (1998) has questioned the value of experimental design, pointing out that even with positive evidence that chimpanzees chose the 'knower' in the guesser-knower paradigm, the difference between the mentalistic and behaviouristic hypotheses concerns "what is known," not about whether the subjects learned to discriminate the eyes as the salient cue (Heyes, 1998, p. 109). Therefore, behavioural evidence for choosing the 'knower' does not reliably indicate the mental state attribution capacity of the subject (Itakura et al., 1999 echo this sentiment): the type of data collected cannot be interpreted to differentiate between behaviouristic and mentalistic hypotheses.

In an object-choice experiment by Call et al. (1998), chimpanzee subjects performed above chance at using a human experimenter's gaze cue to find food in tubes and behind barriers; but not for food under opaque bowls. The authors explain the contradicting results by emphasizing the subjects' interest in foraging in tubes and around barriers, paired with the stimulus enhancement effect of the experimenter's gaze (the experimenter could see the bait in the tube and behind the barrier at the time the cue was given) as likely important factors in the results. Though the experimental results could not allow the authors to choose between an orientation and foraging preference hypothesis, and a hypothesis that the chimpanzees understand 'seeing' as a meaningful property in others, they raised the important issue of ecological validity in studies of this kind.

C. Ecological Validity

There are other criticisms of ecological validity in the guesser-knower paradigm. Firstly, great apes do not interact regularly with humans in their natural habitat and thus should not be expected to be able to follow a human's gaze, much less be able to make any mental state attributions to a human (though they may be able to do these with conspecifics) (Gómez, 1996; Matheson et al., 1998). In addition, eye-gaze cues may be less relevant than

head orientation cues for primates to determine others' direction of attention (Tomasello et al., 2007). Secondly, in the wild, great apes compete over food resources and rarely cooperate (Hare, 2001). It is highly unlikely that a chimpanzee would deliberately point out a monopolisable food source to a competitor with the intention of sharing the food (Hauser & Wrangham, 1987; Hauser, 1997; Hare, 2000, 2001). Therefore, primates' ability to understand gaze cues has not evolved in the context of cooperation (Tomasello et al., 2007). In reaction to this critique, researchers returned to a competitive, conspecific methodology to evaluate the same skills of understanding seeing and knowing (Hare et al., 2000, 2001; Hare, 2001; Hare & Tomasello, 2004). This represents a major paradigm shift in the field, which has shown positive results.

D. Are Eye-Gaze Cues Salient?

The eyes play a special role in social interaction: observing another individual's eye movement can reveal their focus of attention, emotional valence, the social exchange of information, and changes in the individual's motivation (Emery, 2000; Kaplan & Rogers, 2002; Shepherd, 2010). In some primates, eye gaze is not necessarily always congruent with head orientation (Kaplan & Rogers, 2002; Bethell et al., 2007). However, the eyes are not the only source of information about the direction of attention: in the absence of eye cues, head orientation and even quadrupedal body posture are often sufficient communicative cues (Emery, 2000; Langton et al., 2000; Kaminski et al., 2004).

Hietanen (2002) and Shepherd and Platt (2008) showed that for humans and ringtailed lemurs (respectively), cues from head orientation override body orientation. Kaplan and Rogers (2002) and Tomasello et al. (2007) demonstrated that orangutans and chimpanzees (respectively) respond better to cues from head orientation rather than eye direction, whereas Bethell et al. (2007) argue that for chimpanzees, eye gaze may be salient when different from head orientation. Bethell et al. (2007) studied the signal value of chimpanzee eye-gaze as distinct from head orientation. Human observers were able to reliably detect and code three types of gaze; the researchers found that gaze was often incongruent with head orientation, including during a majority of glances (70-100%, a single movement of less than one second), most of scans (42-49%, continuous movement), and some fixations (12-21%, no eye movement). From these observations, the authors concluded that for chimpanzees, another individual's eye gaze cue could be valuable above and beyond information gained from noticing their head direction. The results from Povinelli and Eddy's (1996) begging choice

experiment, in which chimpanzees begged from human experimenters with different combinations of eye contact and head movement, could not differentiate conclusively whether chimpanzees understood gaze from the eyes or the head.

A few studies have systematically analysed all possible combinations of three types of orientation: body, head, and eyes. Emery (2000) and Langton et al. (2000) review work from Perrett et al. (1992) that showed that cells in the macaque superior temporal sulcus recognise and react to congruent combinations of orientations of body, head, and eyes. Perrett and colleagues suggested primates have a “direction of attention detector” in which signals from the eyes hierarchically override signals from head direction, which in turn override signals from body direction. However, experimental studies show that primates use head direction as the most common cue for determining gaze direction. Reaux et al. (1999), in a continuation of Povinelli and Eddy (1996a), found that chimpanzees choose to beg from human experimenters by using a ‘face rule,’ i.e. *choose the person whose face I can see*, rather than a more specific ‘eyes rule,’ i.e. *choose the person with open eyes*. Thus, their results indicated that head cues overrode cues from body orientation and eye direction, except in one critical condition in which subjects begged from a forward-facing person with closed eyes instead of a person with open eyes looking over her shoulder. Follow-up results from Kaminski et al. (2004) support this: the authors argue that the subjects chose the person more disposed to hand over food. In another follow-up, Bulloch et al. (2008) found contrasting results, and suggested that enculturated chimpanzees may have different abilities of understanding human visual attention. Seyama and Nagayama (2005) tested humans in a cuing task and found that there was an additive effect of cues in determining gaze direction: reaction times were shorter when the eyes and head pointed to the same direction, and when the torso was aligned to a different direction; this suggests that certain body parts only relate when they are incongruent.

1. Cooperative Eye Hypothesis

Across studies, humans are consistently found to pay most attention to the eyes, and it is interesting to note the unique morphology of human eyes compared to all other primates. Kobayashi and Kohshima (2001) studied and compared eyes in 88 species of primates, and explained how the features of human eyes, such as horizontal elongation, are adapted for extending the visual field in the horizontal plane by eye movement as opposed to head movement. They suggested that pigmentation of the sclera evolved in primates to hide gaze

direction from others (including predators), and that human eyes, which are highly visible due to their lack of pigmentation in the sclera, are secondarily adapted to enhance gaze cues during cooperative interactions such as group hunting.

More recently, Tomasello et al. (2007) integrated information on eye morphology and gazing behaviour to propose the ‘cooperative eye hypothesis,’ which suggests that humans’ white sclera evolved to improve cooperative and communicative interactions, such as joint attention and pointing. To test this hypothesis, they compared how human infants (12 and 18 months of age) and adult apes followed the gaze of a human model, who looked up to the ceiling either with his eyes only, head only, or both. When the orientations of head and eyes were contrasting, human infants acted in the opposite manner from apes: apes relied mainly on head movement when following gaze, whereas human infants followed only the eyes (Ontogeny may play a role in learning the importance of gaze cues, because enculturated apes are better at following human-given eye cues; see Kaminski et al., 2004). The authors remarked that individuals in a competitive population such as a chimpanzee group should not evolve the morphology of white sclera to allow others to follow their gaze. Kobayashi & Hashiya (2011) elaborated in their gaze-grooming hypothesis that darker sclera allow an individual to access social information through visual scanning without being noticed by others, thus implying the ability to take advantage of others’ cues. However, they also remark that human gaze can be used in a deceptive context, despite the high visibility of the iris within the eye outline.

2. Gazing Patterns in Chimpanzees and Humans

Recent advances in gaze tracking technology have allowed further exploration into the question of how chimpanzees and humans view pictures of faces. Kano and Tomonaga (2009, 2010, 2011) used remote gaze tracking technology to collect data on the gaze patterns of chimpanzee and human subjects looking at photographs of chimpanzees, humans, and other mammals. Both humans and chimpanzees viewed the face region of the photos more than other regions, but human subjects looked significantly longer at faces than chimpanzee subjects did (though Hattori et al., 2010, showed that chimpanzees look longer at chimpanzee faces than at human faces). This suggests that chimpanzees, like humans, have voluntary control of eye movement, and tend to focus on areas with more semantic information available. When looking at facial photographs with species-specific facial expressions, humans consistently viewed the eye region, across species and expressions. Chimpanzees

looked at the mouth area more than humans did, and looked at the mouth more than the eyes in four of eight facial expressions, possibly indicating species-specific strategies for facial communication.

Additionally, Paukner et al. (2007), Goossens et al. (2008), and Teufel et al. (2010) have shown that three macaque species follow the gaze of a model quicker when the model makes a species-specific facial expression related to third-party interactions. This may indicate that gaze following is less a mechanistic orienting response than a cognitive ability under some flexible control that is dependent on the social context. Micheletta and Waller (2012) argue that tolerant macaques follow the gaze of friends with shorter latency than the gaze of others, perhaps because friends are more likely to both benefit from information gained through the gaze following response (such as locating food) when competition between them is reduced. The same mechanisms may affect chimpanzee gaze patterns.

E. Experimental Review of Chimpanzee Food Competition

Hare and Tomasello (2004) tested chimpanzees in the guesser-knower object choice paradigm using both a cooperative human demonstrator and a competitive conspecific model. Both provided a social cue to the experimental subject that on the surface appeared similar: the human pointed with extended arm, and the chimpanzee reached for the baited cup. Subjects found more food in the competitive context compared to the cooperative one.

A series of papers (Hare et al., 2000; Hare et al., 2001) examined chimpanzees' understanding of the visual perspective of conspecifics, and demonstrated that chimpanzees use their experience with what their competitor has seen during the baiting procedure to devise their own competitive strategies. In their experiments, a dominant and a subordinate chimpanzee were each situated at opposite ends of three adjacent cages. The subordinate watched as a human experimenter placed one or two food items in the central cage, whereas the dominant in the cage across from her did not witness the baiting procedure. Both chimpanzees entered the central cage to compete for the food. The pieces of food were placed in a configuration relative to different barriers such as a wall, a tyre, and opaque and transparent occluders, so that either one or both pieces were visible to the dominant as he entered the central cage. The subordinate therefore had seen one food item placed that was hidden from the view of the dominant. On later trials, the dominant witnessed part of the baiting procedure in certain conditions, so that he was either fully informed, uninformed, or misinformed of the final location of one of the hidden bananas. The subordinate was again

allowed to watch the full baiting procedure and thus she could monitor what the dominant had seen on each trial. In all of the experiments, subordinate subjects retrieved significantly more of the food that only they had seen in its final location compared to food that was also visible to the dominant (but see Karin-D'Arcy & Povinelli, 2002 for a replication of the experiments with the approach as the measure, rather than final food retrieval).

The series of Hare et al. experiments sequentially ruled out alternative explanations for the subordinate's behaviour: subordinates were given a head start to address whether they had been reading dominants' intention movements; dominants' doors remained closed during baiting to rule out an intimidation hypothesis; food was hidden behind a transparent barrier to test whether simply the presence of a barrier made food less accessible to dominants, whether or not it was visible. In a follow-up experiment, Kaminski et al. (2008) ruled out another alternative for the subordinate's behaviour of avoiding the visible food: the "evil eye" hypothesis. The evil eye hypothesis proposed that subordinates should avoid any food that the dominant has seen, and should therefore only reach for food that the dominant has not seen at all during baiting. Overall, results showed that the subordinate behaved in a way that indicated that chimpanzees know what others have seen, and modify their own behaviour to maximise food intake by choosing the food the dominant had not seen, rather than competing for the visible piece.

F. Summary

The ability to follow gaze underlies other cognitive abilities, such as the attribution of attention, and may relate to the attribution of knowledge. While initial experiments showed that chimpanzees can follow conspecific gaze, as well as the gaze of a human demonstrator, experiments in the guesser-knower paradigm could not confirm whether chimpanzees were able to gain useful information by following gaze, or whether they understood anything about the connection between the overt behaviour of *seeing*, based on the direction of attention originating from the open eyes, and the mental state of *knowing*. More detailed studies of how chimpanzees view faces, and view eye direction relative to head direction, showed that head orientation is a stronger cue for determining gaze direction that often overrides eye gaze cues. The cooperative eye hypothesis suggested that humans evolved in a cooperative context to more effectively use eye gaze cues. Competitive conspecific studies with chimpanzees effectively demonstrated chimpanzee visual perspective taking, but the question remains as to what chimpanzees know about others' knowledge.

V. Informed Forager Paradigm

In the informed forager paradigm, a subordinate individual is shown the location of a hidden food item, and then released into an arena to search with an ignorant dominant competitor (Menzel, 1974). The dominant can easily exploit the foraging success of the subordinate through physical or social pressure (Baker et al., 1981; Rohwer & Ewald, 1981; Barta & Giraldeau, 1998); thus the subordinate has a high incentive to prevent the dominant from finding the food. Many species have been tested in this paradigm for their understanding of what the other partner knows, based on what she has seen during the baiting procedure. I focus on the informed forager paradigm because it is a naturalistic experiment, within the ecologically valid context of competition (Hare, 2001) that has the potential to reveal how subjects with different levels of knowledge behave to conceal or reveal that knowledge to competitive partners.

A. Menzel (1974)

Strikingly, the narrative of the competition between two chimpanzees Belle and Rock raised interesting questions about intentionality in primates. Their interactions (described in Chapter 1: Introduction) indicate that each chimp was employing tactics and counter-tactics to maximize their rewards. They both acted with the intention to achieve the goal of the food reward and flexibly reacted to their partner's behaviour. Exactly how they did so, the ontogeny of the tactics, was left unspecified.

B. Ducoing and Thierry (2003, 2004)

Similar interactions have been described in a variety of species tested in this paradigm. Ducoing and Thierry (2003, 2004) observed Tonkean macaques' (*Macaca tonkeana*) use of behavioural tactics—such as pauses, avoiding being followed, stopping when being watched, and walking in the wrong direction—which functioned to withhold information from a dominant, uninformed partner. They conclude that the subjects could have modified their behaviour based on simple decision rules rather than any intentional action to modify the behaviour of the partner.

C. Held et al. (2000, 2002, 2010)

A series of experiments conducted with domestic pigs (*Sus scrofa*), showed that both partners modified their foraging behaviour depending on the conditions. Ignorant dominants developed a strategy of exploiting informed subordinates by following closely and scrounging for food (Held et al., 2000), and informed subordinates were more likely to

approach the baited bucket when the dominant was farther from it than the subordinate, and more likely to change direction to move towards the baited bucket when the dominant was moving away and out of the subordinate's sight (Held et al., 2002). Furthermore, subordinates adjusted their behaviour if their partner was more likely to exploit compared to a non-exploiting dominant by losing their initial preference for retrieving a larger reward first (Held et al., 2010). Learning over trials could not predict the subordinates' behaviour, and crucially, the subordinates were not able to avoid the dominants' exploitation. The analyses clearly showed the contingencies between two partners' foraging strategies, and that each partner acted flexibly to achieve the goal of finding the food.

D. Coussi-Korbel (1994)

Coussi-Korbel (1994) described how an informed subordinate male white-collared mangabey (*Cercocebus torquatus torquatus*), Rapide, took an indirect route and delayed approaching the rewarded box in the presence of a dominant, Boss. The subordinate quickly returned to the baited location while the dominant searched elsewhere; Coussi-Korbel noted that rather than simply avoiding Boss, Rapide's behaviour effectively misled Boss, to his own advantage.

E. Bugnyar and Kotrschal (2004)

An experiment with ravens (*Corvus corax*) demonstrated a similar behavioural pattern in a subordinate, Hugin, who created a diversion by searching in unrewarded boxes, which encouraged a scrounging dominant, Munin, to follow (Bugnyar & Kotrschal, 2004). Hugin could have learned this over successive trials, and his tactic allowed him to return to obtain the reward from the correct box without Munin (who was busy searching in the incorrect boxes) exploiting and scrounging from him. Munin soon learned not to follow Hugin. The authors determined that the ravens were responding directly to their partner's behavioural cues, and argued that the ravens' behaviour was intentional "in the sense that he had an intermediate goal to modify the perceptions or experience of his competitor so that his behaviour is then altered" (Bugnyar & Kotrschal, 2004, p. 75).

F. Hirata and Matsuzawa (2001)

Hirata and Matsuzawa (2001) reported on two more chimpanzee dyads that competed in the informed forager paradigm. The uninformed chimpanzee did not have visual access to the baiting, but could observe that the first chimp watched as food was hidden. When a female Pendesa was uninformed, she approached her partner Chloe's route and looked at her

frequently, and soon began to run ahead of Chloe's path. Chloe reacted by walking an incorrect path, and Pendesa again adjusted her movement to match Chloe's. Another participant, a female named Pan, adopted a strategy of searching every location in quick succession without monitoring her partner.

VI. Deception

A. Tactical Deception

Many of the interactions described in the informed forager are considered evidence for intentionality in tactical deception. Byrne and Whiten (1988) defined tactical deception as “acts from the normal repertoire of the agent deployed such that another individual is likely to misinterpret what the acts signify, to the advantage of the agent” (Byrne & Whiten, 1988, p. 271). Whiten and Byrne (1986) and Byrne and Whiten (1990) compiled a catalogue of records (no longer anecdotes in the pejorative sense, as these records were collected by experienced observers) of tactical deception in primates and later argued in favour of representing behaviour using psychological terms, claiming that “a psychological representation is an economical one” (Whiten & Byrne, 1988; see also Whiten, 1993; Byrne, 1997). This functional definition leaves out intention as it is commonly understood because it is often difficult for an observer to distinguish between levels of intentionality. Behaviour with first-order intentionality is meant to affect the other's behaviour: an individual has beliefs and desires about the world, and represents goals, but is unaware of others' mental states; e.g., an alarm call that could mean ‘I want you to run to safety!’. Behaviour with second-order intentionality is meant to affect the other's mind: an individual represents the mental states of others, and understands the effects of his or her own behaviour on others; e.g., an alarm call that could mean ‘I want you to know there is a predator!’. It is difficult to distinguish between the two because the outcome produced in the receiver of the signal will be the same: the listener should run to safety, whether or not he believes a predator is present (Premack, 1988; Coussi-Korbel, 1994; Ducoing & Thierry, 2004; Bugnyar & Kotrschal, 2004). Zero-order lacks intentionality altogether, and can include examples in which the ethologist's definition of a particular behaviour is unclear, an interaction between individuals results in a coincidental gain for one, or manipulation occurs without deception (Byrne & Whiten, 1992). Acts of tactical deception are intentional in the sense that the agent acts in such a way as to achieve a goal; it is additionally possible that an agent intends for his actions

to create a false belief in the dupe (second-order intentionality), though the agent's mental states can not be empirically determined (Byrne, 1997).

B. Forms of Deception

Byrne and Whiten (1990) solicited colleagues via questionnaire to submit observational data on deceptive instances in primates, which were compiled in a database of 253 unique examples. Each record was given a label for its level of deception, based on whether there was a possibility the tactic had been learned, how many times a tactic was used, whether the agent's behaviour was different from normal, whether the dupe distinguished situations in which it had been deceived, and whether there was evidence of intentionality or mindreading, and whether any counter-deceptive tactics were used. Then each record was categorized into one of nine categories, each with sub-categories. The main categories included: Negative, Concealment, Distraction, Concealment & Distraction, Attraction, Creating an Image, Deflection, Using a Social Tool, and Counterdeception. Certain tactics were observed more frequently in the experiments I conducted that deserve deeper explanation to provide context for the empirical data that follow in later chapters.

1. Concealment

Primates can use the tactic of concealment by inhibiting interest in an object. For example, a chimpanzee informed of the location of a hidden food may delay approaching the food in the presence of a partner, or stop short of arriving at the food; these tactics are usually in combination with avoiding gazing towards the food. In this way, the chimpanzee can avoid drawing attention to the food, thus serving to prevent the partner from finding it.

2. Distraction/Attraction

An agent can use misleading tactics by leading a partner away from an object of interest (distraction) or by moving towards an object of interest (attraction) which functions to take the partner's attention away from the agent's goal. For example, a chimpanzee informed of the location of a hidden food may walk away from the food when a partner is following. Alternatively, the informed chimpanzee may lead the partner to a less desirable food item (distraction) before returning to the preferred reward while the partner is occupied.

3. Creating a Neutral Image

An informed chimpanzee can also engage in the tactic of creating a neutral image, behaving in a way that does not indicate to the partner that there is anything of interest in the enclosure to search for. To carry out this tactic, the informed chimpanzee may walk around

the perimeter of the enclosure one or more times, without searching for or gazing towards the hidden reward.

C. Does Deception Involve Mind-Reading?

It is still the subject of debate whether tactical deception is intentional: Byrne and Whiten's (1990) "Level Two" deception implies that the agent can represent others' mental states and understands the mechanism of his deception. They classified the interaction between Belle and Rock in Menzel's original study as Level Two intentional deception. This classification is the basis for further exploration into deceptive tactics in chimpanzees in my study, especially regarding how their tactics are acquired and employed. Also a good diagnostic of mindreading in deception is to be found in the dupe: whether the dupe behaves with "righteous indignation" or attempts to counter the agent's deception (Byrne & Whiten, 1991, p. 129).

VII. Conclusion

During social interactions, primates are known to be flexible and adjust their goals in reaction to the behaviour of their social partner (Humphrey, 1976). It would be a competitive advantage, therefore, to be able to predict a partner's future behaviour (Whiten & Byrne, 1988). Humans are able to predict others' behaviour by attributing mental states such as desires and intentions to them, an ability called Theory of Mind (Dennett, 1971, 1987; Premack & Woodruff, 1978; Leslie, 1991; Baron-Cohen, 1995). But do non-human primates consider mental states as the cause of behaviour, and can they attribute mental states to others? (Premack and Woodruff, 1978; Cheney & Seyfarth, 1990).

There are two main sides to the debate over mental state attribution in primates. Behaviourists argue that only visible behaviour should be described, without additional attribution of mental capacity (Skinner, 1984; Bennett, 1991; Heyes, 1987; 1998), whereas Mentalists argue that primates do exhibit some theory of mind-type capacities and that describing them using psychological terms makes sense (Bennett, 1978; Premack and Woodruff, 1978; Whiten & Byrne, 1988; Whiten, 1993; Byrne, 1997; Byrne & Bates, 2006). Rather than question if animals have a full, human-like ability to attribute mental states to others, most studies have focused on which attributional abilities, if any, non-human primates have (Povinelli et al., 1990; Povinelli & Eddy, 1996).

I believe that chimpanzees should be treated as psychological agents that behave flexibly in social situations, and though they do not have full human-like theory of mind, they may understand some psychological states and may be able to make some attributions (Premack, 1983; Tomasello et al., 2003). However, in agreement with Tomasello and Call (1997) and Hare et al. (2001), the focus of my dissertation is not on *what* chimpanzees know, but rather *how* chimpanzees gain knowledge.

Understanding gaze plays a critical role in gaining information regarding others' attentional states and their focus of interest (Emery, 2000). A proximate benefit of following gaze is gaining information about one's surroundings, for example the presence of food, a potential mate, or a predator. Ultimately, understanding someone else's gaze, what they see, aids in attributing what they know (Povinelli et al., 1990; Hare et al., 2000; Hare et al., 2001); this can affect how one predicts how the other will behave in that context, or how one will modify one's own behaviour.

In the begging and object-choice paradigms, chimpanzees were largely unable to discriminate a human experimenter's eyes as the most salient cue determining their level of attention, though there were methodological challenges concerning the ecological validity of a cooperative communicative cue given by a human experimenter (Povinelli et al., 1990; Reaux et al., 1999; Hare & Tomasello, 2004). In several studies contrasting head orientation with eye direction, primates more reliably followed human demonstrators' gaze by following the orientation of the head, whereas humans followed gaze originating from the eyes (Povinelli & Eddy, 1996; Reaux et al., 1999; Hietanen, 2002; Kaminski et al., 2004; Seyama & Nagayama, 2005; Tomasello et al., 2007; Shepherd & Platt, 2008; Bulloch et al., 2008). Head orientation and even quadrupedal body posture are often sufficient communicative cues of gaze direction (Emery, 2000; Langton et al., 2000; Kaminski et al., 2004). Gaze tracking studies highlighted the different photograph-viewing strategies between humans and chimpanzees: while humans focused their attention on the eyes, chimpanzees preferred to look at the mouth of conspecifics (Kano & Tomonaga, 2009, 2010, 2011), which may be a reason that chimpanzees did not understand the importance of the humans' eye gaze in object choice paradigms. Furthermore, Tomasello et al. (2007) suggested that eye gaze cues may be less salient due to primates' pigmented sclera (Kobayashi & Kohshima, 2001), and that humans may have evolved un-pigmented sclera in a cooperative, communicative context.

Against a competitive conspecific, chimpanzees were able to adjust their own behaviour in relation to what they had seen, and what they knew of what a competitor had seen regarding the location of hidden food items (Hare et al., 2000, 2001). The experiments demonstrated that chimpanzees know what others see, and hence what they know. They did not, however, address *how* the subjects gained visual information in the experiment, only how they did not (by ruling out intimidation hypotheses, etc.).

Further investigation into how primates understand conspecific gaze can reveal whether they attribute knowledge to a group-mate that has seen a hidden food item: the “ability of the target to follow the agent’s gaze is certainly a good candidate for second-order representation, for in doing so it is as if the target were able to see the world through the eyes of the agent” (Whiten & Byrne, 1988). If chimpanzees are able to follow gaze, and attribute knowledge to a competitor in this way, they may be able to alter their own behaviour to take advantage of the other’s knowledge, and additionally to counter this exploitation with tactical deception. This is the premise for the current empirical study of the informed forager paradigm described in the following chapters. I address the questions of whether an informed partner gazes towards a hidden food item, potentially revealing information to her competitor; whether the competitor follows her gaze to gain information about the food; and if the informed partner withholds a gaze cue from her competitor.

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I. Informed Forager Methods Introduction

Menzel introduced the informed forager paradigm in a series of experiments published in his chapter “A Group of Young Chimpanzees in a One-Acre Field” (1974). The general procedure of his experiment was to inform a chimpanzee ‘leader’ of the location of a hidden item in the group’s outdoor enclosure—either a desirable piece of food or toy, or a frightening toy snake. After the baiting took place, the leader was released into the enclosure with the rest of the social group to search for the hidden item(s). Menzel recorded the interactions of the group members in relation to each other’s behaviour, the incentive structure of the hidden items, and the dispersion of the items.

In several other studies in the informed forager paradigm, numerous containers such as boxes or film canisters were placed in the subjects’ living area as hiding locations for the food (Coussi-Korbel, 1994; Held et al., 2000; Hirata & Matsuzawa, 2001; Bugnyar & Kotrschal, 2004). However, Hirata and Matsuzawa (2001) report that the dominant individual in their study gained information from the subordinate regarding her direction of movement, and as she was familiar with the experimental boxes, would run ahead of the subordinate toward the box in her line of travel. It was a very clever strategy on the part of the dominant to gain information about the food’s location in this way, as it made it difficult for the subordinate to withhold information and even more difficult for her to approach the food without high risk of losing it to the dominant.

For the purpose of the current experiment, I did not want the experimental setting to be too easy for the dominant to assess where the food was without genuinely searching, as in Hirata and Matsuzawa (2001). The subordinate should have sufficient opportunity to win the reward often enough to stay motivated to participate. Therefore, food was hidden at fixed locations but in more natural conditions: boxes specific to the experiment were not set up in the enclosure, rather, food was hidden using the natural features of the enclosure, for example in a tyre or under a barrel.

Another change that was made to the procedure was that the dominant was released from her cage before the subordinate into the outdoor enclosure. In Hirata and Matsuzawa (2001), the chimpanzees were moved into the same cage before release, because Menzel (1974) had not found conclusive evidence to suggest that the knowledgeable individual communicated about the food to it’s partner(s) before their release. Therefore, whether the partners were together or each in their own cages at the time of their release did not influence

whether the ignorant partner found the bait. In some of Hare's experiments (Hare et al., 2000, 2001), the subordinate was released for competition before the dominant to control for the subordinate simply reacting to the dominant's direction of movement. However, in my experiments, the dominant was not informed of the location of the hidden food (except in one control condition) and thus the subordinate was not expected to read the dominant's behaviour before entering the enclosure. Therefore I decided it would be best to release the ignorant dominant first. Additionally, a few of the hiding places were relatively close to the release doors, and I feared due to the delay in opening the hydraulic doors, that if the subordinate was released first, she might be able to find the bait at these closer locations before the dominant had time to assess the situation.

II. Methods: Informed Forager Experiment 1: *Competition*

A. Subjects

Captive chimpanzees (*Pan troglodytes*) housed at the Living Links Center, Yerkes National Primate Research Center Field Station at Emory University in Lawrenceville, Georgia, participated in this study. At the Field Station there are two groups, FS1 and FS2, each of which comprises eleven individuals (Tables 3.1, 3.2): these chimpanzees have been housed together since the 1970s and 1993, respectively (Seres et al., 2001).

Table 3.1: Chimpanzees at Yerkes FS1, from most dominant to least dominant

Name	Group	Sex	Birthday	Rearing History	Kinship
Socko	FS1	M	23 Jan 1987		Half-brother of Donna
Georgia	FS1	F	27 Aug 1980	Mother/Group	Daughter of Borie, sister of Rita, mother of Katie
Borie	FS1	F	1 Jan 1964	Mother/Group	Mother of Georgia, Rita, grandmother of Katie, Tara
Donna	FS1	F	3 Apr 1990	Mother/Group	Half-sister of Socko
Katie	FS1	F	10 May 1989	Mother/Group	Daughter of Georgia
Rita	FS1	F	23 Sep 1987	Mother/Group	Daughter of Borie, sister of Georgia, mother of Tara
Anja	FS1	F	9 Jan 1980	Mother/Group	No kin in group
Reinette	FS1	F	17 Dec 1987	Mother/Group	No kin in group
Mai	FS1	F	1 Jan 1964	Mother/Group	Mother of Missy
Tara	FS1	F	5 Sep 1995	Mother/Group	Daughter of Rita
Missy	FS1	F	8 Jul 1993	Mother/Group	Daughter of Mai

Table 3.2: Chimpanzees at Yerkes FS2, from most dominant to least dominant

Name	Group	Sex	Birthday	Rearing History	Kinship
Steward	FS2	M	8 Sep 1993	Mother/Group	Son of Vivienne
Chip	FS2	M	30 Mar 1989	Nursery/Group	No kin in group
Ericka	FS2	F	20 Oct 1973	Home/Nursery	No kin in group
Cynthia	FS2	F	7 Jun 1980	Nursery/Group	Mother of Virginia
Vivienne	FS2	F	27 Jul 1974	Nursery/Group	Mother of Steward
Barbie	FS2	F	14 Jun 1976	Nursery/Group	No kin in group
Virginia	FS2	F	18 Apr 1991	Mother/Group	Daughter of Ericka
Daisy	FS2	F	1 Oct 1989	Mother/Group	Daughter of Tai, sister of Julianne
Tai	FS2	F	1 Jan 1967	Mother/Group	Mother of Daisy, Julianne
Julianne	FS2	F	15 May 1998	Mother/Group	Daughter of Tai, sister of Daisy
Waga	FS2	F	19 Mar 1982	Mother/Group	No kin in group

Before data collection for the *Competition* or *Unequal Rewards* began, chimpanzees in both groups were tested against a linear dominance hierarchy. Subordinates from each group were then tested for their memory of the placement of banana slices in differently coloured tubes, and then different buckets (See Appendix 3); both those experiments were unsuccessful for various reasons. It became clear that changes to the finalised protocol of the *Competition* and *Unequal Rewards* experiments would reduce the subject pool: only FS1 was used in the final informed forager experiment for reasons related to their housing. At FS1, a small Lexan window was placed into two of the four metallic hydraulic doors—doors 3 and 4—leading out to the enclosure from the ‘Cognition room’; the Lexan replaced a steel plate that had covered the window hole previously (Figure 3.1). However, at FS2, the plastic doors did not have holes in them already; a decision was made not to reduce the integrity of the doors by cutting new holes, or to not replace them altogether with metallic doors. While this problem was potentially surmountable, the issue of space was not: FS2 does not have a ‘Cognition room’ and therefore it was impossible to lock nine chimpanzees into two cages, and use the other three cages for the experiment. Ultimately, FS2 was abandoned as an experimental site. Therefore, Tai, Barbie, and Julianne, who had been tested with tubes and buckets, did not participate in the *Competition* or *Unequal Rewards* experiments.

Pairs of chimpanzees from FS1 were chosen to compete: pairs consisted of captive-born unrelated individuals, taken from the same social group of 11 individuals. In FS1, Missy (age 18) and Reinette (age 23) were chosen as subordinates for the study based on their

positions determined during dominance testing. Hierarchy testing was completed prior to the experiment, and since the hierarchy was not precisely linear, each subordinate was partnered with a dominant competitor that had at least three positions in rank difference, to be sure that one was dominant over the other. Many of the members of the FS1 group are kin, and I avoided pairing related individuals, because mothers and daughters, having shared a close bond throughout child-rearing, might be more tolerant of food sharing (van Lawick-Goodall, 1975). Therefore, Missy was paired with Rita (age 23), and Reinette with Georgia (age 30).

Of the four FS1 subordinates tested during tube and bucket training (See Appendix 3), only Missy and Reinette were included in the final analysis. Of the two females in FS1 that were not included in the final analysis, Katie and Tara, Katie completed all trials for the *Competition* and eight trials in the *Unequal Rewards* condition with her partner Socko. Socko was the only male in the FS1 group, and was very tolerant of food sharing. During group feeding situations, he often let females take food before he ate, and even let some females take food directly from his mouth. During the course of the *Competition*, he did not put enough competitive pressure on subordinate Katie, who won the food reward on every trial. There was no need for her to act deceptively, and on many trials Socko would leave the ‘Cognition room’ but not follow Katie towards the food. Socko was removed from the study after completing eight trials in the *Unequal Rewards* condition. Tara was paired with both Anja and Donna as dominants, but neither were motivated to exit the ‘Cognition room’ on experimental trials. I attempted to pair Katie, as a dominant, with Tara. However, early in the data collection for the *Competition*, the two chimpanzees got in a fight and afterwards would not be locked inside together, and both were thus removed from the study.

B. Setting

Subjects were housed in an outdoor enclosure (24 x 30 m) and had access to two indoor areas, six Bedroom cages (3 x 3 x 3 m), and five ‘Cognition Room’ cages (1.74 x 1.74 x 1.74 m) (See Figure 3.1). There were mesh panels in the ‘Cognition Room’ between cages 1 and 2, and 2 and 3, measuring 28.5 by 20.5 inches. Most cages in each building had hydraulic doors connecting them, as well as hydraulic doors leading out to the enclosure. In the ‘Cognition Room’, a small Lexan window was placed into two of the four doors leading out to the enclosure, doors 3 and 4. The outdoor enclosure contained a three-story climbing structure with ladders and ropes, as well as several tyres, kegs, barrels, and other enrichment objects. All chimpanzees were fed twice a day with chow, fruit and vegetables, and water

was available ad libitum. Chimpanzees were not deprived of food at any time and were not subject to any invasive procedure.

Testing took place in the 'Cognition Room' and in the outdoor enclosure at FS1. All of the chimpanzees in the group were locked inside so that a human experimenter (E1) could enter the enclosure safely to hide a banana on each trial. Non-participating chimpanzees were called into the Bedroom area and came in voluntarily, and were rewarded with a quarter slice of apple. They could not witness the baiting procedure from the Bedroom cages. For maximum safety, chimpanzees in the Bedroom area were locked in Cage #6, which was also at a 90-degree angle to the enclosure, behind Cage #5. When necessary, hydraulic doors leading to the enclosure were pinned and locked from the inside of enclosure.

Each pair was tested separately. While baiting took place, the participating chimpanzees were locked in the 'Cognition Room': the informed subordinate subject was always in the third cage with the Lexan window to the enclosure, the Knowledge Cage #1, and the uninformed dominant competitor was always in the second cage without a window, the Ignorance Cage. Each chimpanzee could see her competitor through the mesh panel between the two cages, and the dominant was able to see that the subordinate had a window; however, the dominant could not see out the window from the Ignorance Cage. The first cage was always left empty so that E1 could enter the enclosure through the hydraulic chimpanzee door. After baiting was complete, both partners were released into the outdoor enclosure to search for the hidden food on each trial.

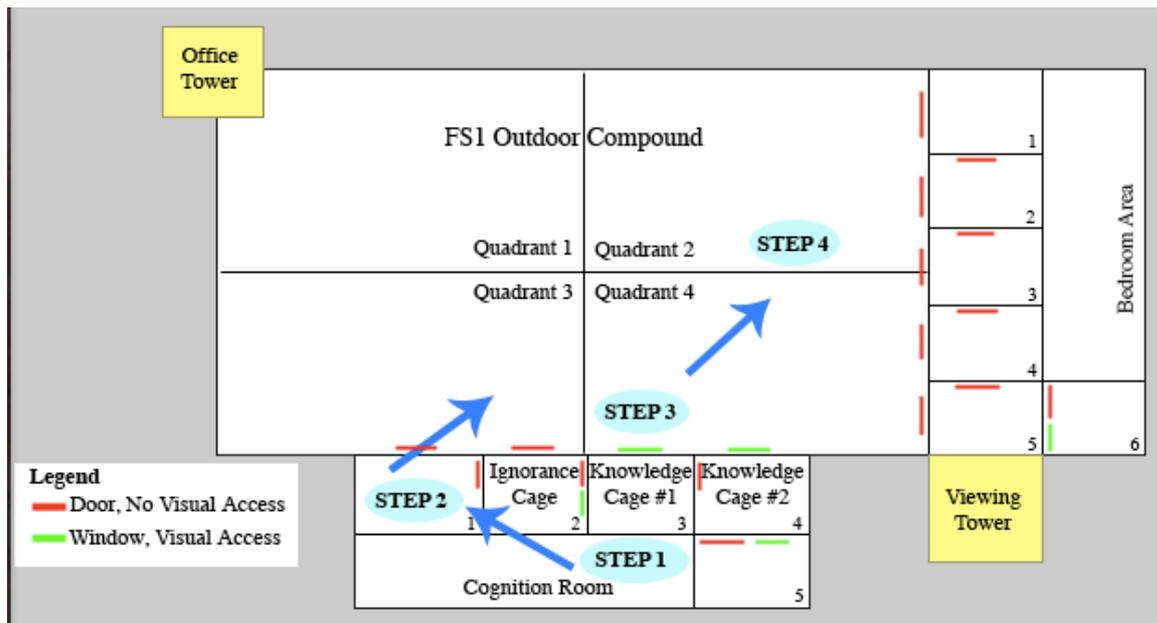


FIGURE 3.1: Diagram of the Testing Area and Procedure

C. Apparatus

At FS1, a small Lexan window was placed into two of the four metallic hydraulic doors, doors 3 and 4 (also known as Knowledge Cages #1 and #2), leading out to the enclosure from the ‘Cognition Room’; the Lexan replaced a steel plate that had covered the window hole previously.

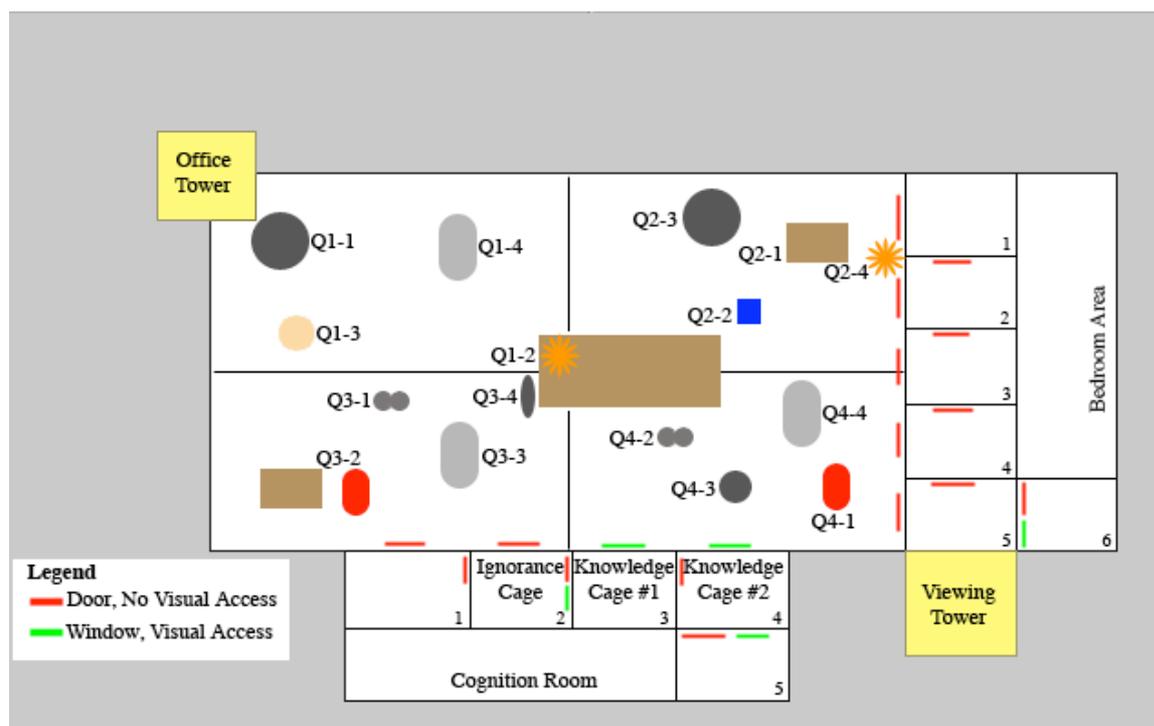
D. Experimental Design

This aim was to test whether the dominant could pick up on movement and gaze cues from the subordinate in order to find the hidden food, and whether the subordinate could avoid this type of exploitation by withholding these cues. I predicted, based on previous studies in this paradigm, that the subordinate would successfully recover the banana on several early trials until the dominant learned a strategy such as following the subordinate and then taking the food; at this point, I predicted that the subordinate would develop a counter-tactic such as delaying her approach to the food.

I considered the outdoor enclosure as comprised of four approximately equal quadrants, and there were four hiding places in each quadrant, for a total of sixteen hiding places. The baiting schedule cycled through the first place of each of the four quadrants, then the second place of each quadrant, and so on (Quadrant 1-Place 1; Quadrant 2-Place 1; Quadrant 3-Place 1; Quadrant 4-Place 1; Quadrant 1-Place 2, Quadrant 2-Place 2...) (See Table 3.3 and Figure 3.2).

TABLE 3.3: Hiding places in each quadrant

Quadrant	Place 1	Place 2	Place 3	Place 4
Q1	Tire	Hose nozzle	White barrel	Culvert
Q2	Ladder joint	Tower	Tire	Behind lixit
Q3	Kegs	Red ring	Culvert	Hanging tire
Q4	Red ring	Kegs	Small tire	Culvert

**FIGURE 3.2:** Schematic diagram of the locations of hiding places within the enclosure

Each subordinate subject underwent testing for baseline behaviour at four hiding places; a banana was hidden in one place in each of the four quadrants. Then during experimental *Competition* trials, each subordinate competed with her dominant partner at every other hiding place, cycling through all sixteen hiding places on the list until twenty competitive trials per chimpanzee pair had been completed (the original four *Baseline* locations were the final four experimental locations). Then, each pair did four *No Knowledge* control trials, in which both animals in the pair were locked together in the Ignorance Cage without the window; neither competitor was informed as to where the banana was hidden to mimic a natural foraging situation. These control trials were followed with four more competitive trials, for a final total of twenty-four competitive trials. Each pair completed

another four control trials in a *Full Knowledge* condition, in which both partners were each locked into a Knowledge Cage with a window to watch the baiting process. Finally, four additional *No Bait, No Knowledge* trials were completed, in which both chimpanzees were again locked together in the Ignorance cage, and no banana was hidden in the enclosure (See Table 3.4).

TABLE 3.4: Number and type of trials, in the order they were completed

Trial Type	Number of Trials
<i>Baseline</i>	4
<i>Competition</i>	20
<i>No Knowledge</i>	4
<i>Competition</i>	4
<i>Full Knowledge</i>	4
<i>No Bait, No Knowledge</i>	4

E. Procedure (for each condition)

1. Dominance testing

Dominance testing took place to directly confirm a previously determined linear hierarchy based on observational data. The test was in a food competition setting, since chimpanzees would be competing for food in the informed forager paradigm. The two competing chimpanzees were each locked in cages on opposite ends of a consecutive three-cage run in the Bedroom area (see Hare et al., 2000). The central cage remained unoccupied, and E1 entered the cage to place a banana in the centre, equidistant from both competitors' hydraulic doors leading into the central cage. Once the banana was placed and all doors locked, the hydraulic doors were opened approximately fifteen centimetres so that each subject could see her competitor, and the banana. Then both doors were opened simultaneously and chimpanzees were allowed to enter the central cage. The chimpanzee that retained the banana was determined to be dominant. Each pair competed for the best score out of three competitions.

2. Baseline testing

For the four *Baseline* tests, only the subordinate chimpanzee subject was locked into the Knowledge Cage #1 in the 'Cognition Room'; the dominant competitor was locked in the Bedroom area, so that she could not learn about the experimental procedure. As indicated in Figure 3.1, during Step 1, E1 stood in front of the subject's cage and showed her the banana

to be hidden. During Step 2, second experimenter (E2) opened the hydraulic door of Cage #1, unlocked both padlocks on the cage door, and then E1 crawled through these doors into the enclosure. During Step 3, E1 approached the subject's Lexan window from the outside enclosure, and called the subject to look through. During Step 4, once the subject was at the window, E1 held the banana up and walked towards the designated hiding place, hid the banana, then held up her empty hands as she walked back to the 'Cognition Room.' E2 closed the hydraulic door and locked the cage behind E1. During Step 5, E1 exited the 'Cognition Room,' ran to the Viewing Tower to set up a video camera, and then ran around to the opposite Office Tower to set up another camera there. Once both cameras were running, E1 radioed to E2 to let the subject out. E2 opened the hydraulic door of Knowledge Cage #1 to release the subject into the enclosure. E1 video recorded the subject's behaviour until the chimpanzee found and ate the bait. At that point, E2 called the subject back into the 'Cognition Room' for a second trial. Two trials were attempted on any testing day because the subject was usually still motivated; third trials were not attempted, because subjects' motivation may have been diminished after eating two whole bananas.

Four *Baseline* tests were conducted to measure the average time to find the reward in the absence of a competitor; gaze behaviour was also recorded, for example, to determine whether chimpanzees looked at things moving around their environment, such as carts driving by, people walking by, or birds flying overhead, all of which occurred frequently in the outdoor testing environment.

3. *Competition: One Reward*

During the *Competition*, I predicted that the subordinate would find a majority of the hidden rewards, but that over time the dominant would become more motivated to exploit the subordinate's foraging success. I predicted that the subordinate would act to avoid this exploitation by withholding information or misleading the dominant away from the bait's location.

For the *Competition*, the dominant competitor was locked in the Ignorance Cage, adjacent to the subordinate in the Knowledge Cage #1. All steps as indicated above in Figure 3.1 occurred in the same order during baiting for the competition. The dominant was released into the enclosure for the competition before the subordinate.

4. *No Knowledge Control Trials*

The purpose of this control was to assess whether the subordinate had any other way of finding the banana, other than prior knowledge or random search, such as using an olfactory cue. Also, I was interested in the dominant's behaviour—would the dominant continue to follow the subordinate? Would the dominant understand the subordinate's lack of knowledge? At what point would the dominant search on her own? I predicted that the subordinate would be less motivated to search for hidden food, and that the dominant would not use the same tactics as during the *Competition* to exploit the subordinate.

For these controls, both chimpanzees of a pair were locked together into the Ignorance Cage without the window, and did not witness the baiting procedure. The baiting procedure was the same as during the competitive trials, except that E1 did not approach the window of the (now empty) Knowledge Cage #1 and call for the subject's attention; E1 went directly to the baiting site in the enclosure, hid the banana, and returned inside. Trials were video recorded and were stopped after five minutes, regardless of whether the banana had been discovered.

5. *Full Knowledge Control Trials*

The *Full Knowledge* controls were conducted to test whether the dominant would adopt the behavioural strategy of following the subordinate if the dominant had information of her own regarding where the food had been hidden. Based on results from previous studies (Coussi-Korbel, 1994; Hare et al., 2000; Hare et al., 2001; Karin-D'Arcy & Povinelli, 2002; Bräuer, et al., 2007), I expected that the dominant would not rely on the subordinate for any movement cue when she had information of her own about the hidden banana.

For these controls, the chimpanzees were locked into Knowledge Cages #1 and #2 in the 'Cognition Room.' This was the dominant's first experience looking through the windows during testing. No *Baseline* training was necessary for the dominants, since they were already familiar with all of the hiding places and the procedure of the experiment; all dominants were keen to look through the window, especially when E1 was in the enclosure. The baiting and recording procedure was the same as the *Competition* trials.

6. *No Bait, No Knowledge Control Trials*

In the original *No Knowledge* control, the chimpanzees searched for a banana despite not knowing its location. The purpose of the *No Bait, No Knowledge* control was to find out whether searching behaviour is contingent upon seeing an experimenter carry a banana into

the enclosure and return empty-handed. At the most basic level, this new control was intended to check that the subjects' searching behaviour was not an automatic behaviour following a period of being locked in the 'Cognition Room,' but rather due to the testing situation. I predicted that the subjects would not search the enclosure.

For this control, the procedure was exactly the same as the original *No Knowledge* control, except that E1 did not show the chimpanzees a banana in Step 1, nor hide one in the enclosure. E1 entered the enclosure, walked around the structure as if to hide something, and then returned to the 'Cognition Room.'

F. Behavioural recording

Each trial was video recorded from two opposite angles; an unmanned Panasonic PV-GS320 video camera was placed on a tripod on the Viewing Tower, and E1 recorded from the Office Tower using a Sony DCR-HC52 and/or Canon Vixia HF100 cameras. Two cameras were used to capture video of the chimps in case an individual was not visible from one position, for example, obscured by an object or structure in the enclosure. The Panasonic camera was set to record the majority of the enclosure's area, whereas the Sony or Canon camera that E1 handled was zoomed in to frame the two competing individuals and record head orientation and gaze interactions, which appear less detailed on the zoomed-out Panasonic tapes.

G. Coding and Video Analysis

Videos were coded using Noldus Observer XT 9 software, licensed to Professor Andrew Whiten. Continuous variables were coded using an instantaneous (every one second) focal sampling method to capture detailed gaze and locomotion behaviour; point variables were coded using the "all occurrences" sampling method (Altmann, 1974). A coding scheme was created based on schemes used by Held et al. (2002), Hirata and Matsuzawa (2001), Ducoing and Thierry (2003).

Behaviours were divided into general categories: Locomotion, Bait Directed, Gaze Behaviour, Proximity Between Chimps, Dominant Distance to Food, Social Interaction, Visual Access to Partner, Gaze Towards Bait, Absolute Direction, Absolute Gaze (See Appendix 2 for the full coding scheme, as well as an ethogram defining each behaviour). Within each category, there were several different mutually exclusive behaviours; for example, in the Locomotion category, No Locomotion, Walk, Change Direction, Not Visible, and so on. Certain behaviours had modifiers associated with them; for example, Walk is

modified by Chimp (Closer/ Further) and Bait (Towards/ Away). Absolute movement codes noted which of the four quadrants the subject was currently in, which quadrant she was moving towards (or, if not moving, a zero was entered), and whether a food item was hidden in that direction. The set of absolute codes is more specific than the relative codes, and it helps to support relative codes.

For the analyses in the following chapters, a selection of the variables was tested (Table 3.5).

Table 3.5: Variables and definitions

Variable name	Definition
Locomotion towards the bait	The subject moved (walk/run/climb) in the relative direction of the hidden food
Gaze towards the bait	The subject directed her gaze in the relative direction of the hidden food
Locomotion towards a quadrant	The subject moved (walk/run/climb) in the absolute direction of a specific quadrant of the enclosure
Gaze towards a quadrant	The subject directed her gaze in the absolute direction of a specific quadrant of the enclosure
Locomotion towards the opponent	The subject moved (walk/run/climb) in the relative direction of the other chimpanzee
Locomotion away from the opponent	The subject moved (walk/run/climb) in the relative direction away from the other chimpanzee
Look at the opponent	The subject looked directly at the other chimpanzee
In the same quadrant	Both subjects are located in the same quadrant of the enclosure
In different quadrants	Both subjects are located in different quadrants of the enclosure
Going towards the same quadrant	Both subjects are moving (walk/run/climb) in the absolute direction of the same quadrant of the enclosure
Change direction	The subject changed her absolute direction of movement
Change gaze direction	While in view of the opponent, the subject changed her absolute direction of gaze
Gaze towards same quadrant	Both subjects directed their gaze in the absolute direction of the same quadrant of the enclosure
Stop locomotion	The subject stopped moving for five consecutive seconds
Stop gaze towards the bait	The subject stopped gazing towards the food for five consecutive seconds
Monitoring glances	The subject looks at the opponent and then gazes towards the bait for two consecutive seconds
Recruitment glances	The subject looks at the opponent and then gazes towards the bait for two consecutive seconds, and stops locomotion for five consecutive seconds

III. Methods: Informed Forager Experiment 2: *Unequal Rewards*

A. Subjects

The same pairs of chimpanzees that participated in Experiment 1 also participated in Experiment 2: Missy and Rita, and Reinette and Georgia.

B. Setting

The setting for the second experiment was the exact same as in Experiment 1: the dominant was locked in the Ignorance Cage of the ‘Cognition Room’ and the subordinate was locked in the Knowledge Cage #1 during baiting. All other chimpanzees were locked into the Bedroom area on the other side of the enclosure where they could not see the experimental procedure.

C. Experimental Design

For this experiment, both a banana and a cucumber were hidden on each trial to determine whether a reward of lower preference, the cucumber, would have an effect on the subordinate’s behaviour. I expected that, though each individual subject preferred banana to cucumber, the knowledgeable subordinate should approach the cucumber before the banana within each trial, with the (learned) expectation that the dominant would follow and subsequently take the reward. Hence, if the dominant took the cucumber, the subordinate would still have a chance to win the banana.

From the original list of 16 hiding places, two places had to be changed due to safety concerns with human experimenters climbing on the structure during baiting: Q1-Hose nozzle became Q1-Hammock, and Q2-Tower became Q2-Box. Once these changes were made, a list of eight pairs of places was devised for hiding bananas and cucumbers. The hiding spots were semi-randomized such that each bait was hidden twice in each of the four quadrants during the first eight trials, then the same list was used for the subsequent eight trials, with the location of the banana and cucumber reversed. Thus, the banana was hidden once in all 16 places, as was the cucumber. Pairs were counterbalanced for side of enclosure: no two rewards were hidden together on the left (Q1, Q3) or the right side of the enclosure (Q2, Q4) because of the possibility that a subject would find the reward closer to their starting position first, regardless of preference.

Once the list was made, the order was again randomized for the pairs of competing chimpanzees, to control for order effects across pairs. An example of the Missy-Rita baiting schedule is printed below in Table 3.6 for trials 1-8; for trials 9-16, the cucumbers were

hidden in the locations in the first column and the bananas were hidden in the locations in the second column (reversed); for the final trials 17-20, the rewards were again hidden in their original order. Each pair competed for 20 trials.

TABLE 3.6: List of hiding places for bananas and cucumbers per trial, Pair 1

BANANA	CUCUMBER
Q4 Small tire	Q1 Hammock
Q2 Tire	Q3 Red ring
Q3 Culvert	Q4 Kegs
Q2 Cone	Q1 White barrel
Q1 Culvert	Q4 Red ring
Q3 Hanging tire	Q2 Ladder joint
Q1 Tire	Q2 Behind lixit
Q4 Culvert	Q3 Kegs

D. Procedure (for each condition)

1. Preference testing

Each chimpanzee subject was individually tested for her preference between banana and cucumber. A subject was locked alone in a cage in the Bedroom area, where preference testing took place. E1 presented a small slice of cucumber and a small slice of banana placed approximately 30 centimeters apart on a sliding tray, which was pushed to the edge of the cage mesh so that the subject could make a choice. Subjects indicated their choice by pointing through the cage mesh to their preferred item. Only one food item could be chosen per trial, and each subject received 10 preference test trials. Of these 10 trials, the side of the tray on which the banana and cucumber were placed was semi-randomized with the condition that the same food item could not be in the same position on more than two consecutive trials; each reward was baited an equal number of times on both sides of the tray. I expected all subjects to prefer banana to cucumber.

2. Unequal Rewards

I predicted that the subordinate would approach the banana first at the beginning of the experiment, and that the dominant would exploit her foraging success. I predicted that after several trials the subordinate would change tactic to approach the cucumber first.

The procedure for this *Unequal Reward* condition was very similar to the previous, one-reward *Competition* condition. The dominant chimpanzee was always locked into the Ignorance Cage, while the subordinate was in the Knowledge Cage #1, and they had visual

access to each other through the mesh panel. E1 showed both subjects the banana and the cucumber, and often allowed them to smell, touch, or take a small bite from the rewards to motivate them to pay attention during baiting.

I anticipated difficulty in hiding two rewards while the subject watched: that either she would stop paying attention after the first reward was placed, or not appear to remember which reward was hidden in which location. Therefore, a second experimenter (E2) joined E1 in the enclosure during baiting. Both experimenters crawled through the door in the first cage of the 'Cognition Room' into the outdoor enclosure; E2 always hid the cucumber first, then E1 hid the banana. E2 approached the subordinate's window, showed her the cucumber, and placed it in its designated hiding location as the subject watched. During this time, E1 waited out of view of the subordinate. As soon as the cucumber had been placed, E1 approached the subject's window to show her the banana and maintain her attention as it was hidden in its place. Often a third experimenter, E3, communicated with E1 and E2 via radio that the subject was paying attention; E3 also helped to control the hydraulic doors.

As before, once both experimenters were back in the 'Cognition Room' with all doors closed and locked, and the video cameras on both towers were recording, E1 radioed to E2 and E3 to simultaneously open the doors to release the chimpanzees into the enclosure.

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I. Abstract

Previous published studies in the informed forager paradigm included narratives describing how an ignorant competitor exploited an informed subject by following her movement and gaze, and how the informed subject avoided this exploitation, for example by walking away from a hidden bait, or by first glancing at her opponent to make sure he was not paying attention before picking up the food. However, analysis with descriptive statistics fails to capture the complexity of these interactions, which ranges from single decision-making points to larger patterns of following and misleading. Reports of the mean percentage of food obtained by each subject, their paths of movement in their enclosure, and percentages of time that either subject followed or gazed towards the other, do not give any indication of the nature or development of the interaction between the competitors. This chapter aims to (i) illustrate the historical progression of statistical analyses of experiments in the informed forager paradigm, (ii) to point out shortcomings in previous analyses, and (iii) to suggest a novel method of analysis borrowed from the field of neurology: cross correlations. Cross correlations reveal the contingent relationships between the subjects' behaviour, as well as how their behaviour changes over the course of the experiment, and are most suitable for demonstrating the detailed interactions that have previously only been evoked by narrative description.

II. Introduction

Menzel (1974) richly described the interactions of his subjects in the informed forager paradigm, and depicted the tactics and counter-tactics that they developed during the competition, some of which have since been described as second-order intentional deception (Whiten & Byrne, 1988a, 1997; Byrne & Whiten, 1990, 1991; Hirata & Matsuzawa, 2001; Ducoing & Thierry, 2003). Menzel includes an evocative account describing the interaction:

“There was a continuous feedback between leaders and followers until the group was within relatively close range of the goal, the leader usually adjusting his rate so as to just barely keep ahead” (Menzel, 1974, p. 134).

Analysis with descriptive statistics fails to capture the complexity of this interaction, from single decision-making points to larger patterns of following and misleading. Some published experiments have merely reported the mean percentage of food obtained by each competitor as evidence that one subject knew what the other had seen (e.g., Hare et al.,

2001), rather than describe the *interaction* of the two competitors. In reporting results from experiments in this paradigm, it is laborious to recount every single interaction; yet it is equally problematic to provide a broad view of behavioural patterns without sufficient detail to understand, for example, whether there was a tipping point at which subjects' behaviour changed. In essence, the dynamic dimension of the interaction, the "continuous feedback" between subjects, is lost in the report of basic descriptive statistics.

While many of the publications on the informed forager paradigm describe interesting examples of tactical deception, many of these are written off as anecdotes. Though examples of tactical deception are rare, and their interpretation often contested, compilations of records systematically collected by experienced observers should be looked at for the underlying behavioural patterns, and the contingent relationships that exist between subjects, in order to show what types of interaction may lead to an act of tactical deception (Whiten & Byrne, 1986; Byrne & Whiten, 1990; Byrne, 1997).

For a paradigm so rich in possible interpretations, the statistics that have been used to describe the interactions seem rather inadequate to provide an informative level of detail when describing the interaction, especially when attempting to parse out more complex interactions such as which cues are more useful to the competitor to gain information about the location of the hidden food. In this chapter, I first discuss the statistical analyses that previous authors have used, and explain their limitations in showing the "continuous feedback" that Menzel and others described. For example, Held et al. (2002) use logistic regression to effectively demonstrate some behavioural contingencies, but their data coded in relative terms (i.e., towards the bait vs. not), and are thus insufficient to understand behaviour that occurs more generally, such as movement in a non-specific direction. Another example is the post-event time histogram, which was introduced by Preuschoft (1992); I propose a limitation that a statistical comparison pre- and post- event is not straightforward. Finally, I describe an elegant solution borrowed from neuroscience that accounts for the various problems encountered: *cross correlations*, with an independent estimation of the potential noise distribution, eliminate the need for a pre- post- comparison, and make the dependent variable interpretable before and after the event—not just the *difference* in behaviour. I explain in detail how the cross correlation statistic is computed, how the correlogram graph is constructed, and how it is tested for significance. Finally, I summarize why this statistic is

highly effective in showing the behavioural contingencies between subjects (and how they change over time) in the framework of the informed forager paradigm.

III. Literature review

A. Menzel's (1974) analysis

Menzel included a series of maps that showed the routes of travel of the animals in his study, comparing experimental conditions to a control in which no chimpanzee was shown the hidden food (see appendix to Chapter 4, Figure 4.1). The tables, graphs, and maps published in the paper do not, however, effectively show the “continuous feedback” between the chimpanzees or how the leader “adjust[ed] his rate” that Menzel described so vividly in the text. It is cumbersome for the reader to interpret so many graphs to gain a full understanding of the interaction, especially since so much information is missing, such as pauses, glances between the subjects, and who found the reward on the trial depicted. Because of this, it is impossible to tell whether the informed leader's changes of direction were due to simpler causes: not remembering the hiding location, or simply trying to avoid the dominant, or whether they reflect the possibility of one subject's intentional misleading of a competitor away from the food, as the textual description might indicate.

B. Ducoing and Thierry's (2003) analysis

Ducoing and Thierry (2003) repeated the informed forager experiment with Tonkean macaques. As Menzel did, they included several maps of their subjects' routes of travel in different trials, and included arrows indicating where different tactics were employed; for example, when the subordinate stopped in order to withhold information if he was monitored by the dominant, or when he inhibited himself from retrieving the food. Printing a small selection of maps from the total collection to convey instances of tactically deceptive behaviour may, however, lead the reader to misunderstand the normal pattern of the interaction and the frequency of such behaviour.

In an effort to describe the “continuous feedback” between subjects as originally described by Menzel, Ducoing and Thierry included a table in their publication listing the percent of time that the ignorant individual spent monitoring the informed subject (see appendix to Chapter 4, Figure 4.2). The authors divided the monitoring behaviour into “following” and “keeping tabs,” the latter defined as when the ignorant opponent could see the informed individual, though was not following. This is a step in the right direction

towards statistically describing visual monitoring behaviour, however, a table containing the duration of time one subject monitored the other would say nothing of whether the other subject was aware that she was being watched, or furthermore, whether it influenced her behaviour at all.

C. Coussi-Korbel's (1994) analysis

Coussi-Korbel (1994) described tactical deception in mangabeys in the informed forager paradigm. She published a table that included the development of the informed subordinate's various actions, for instance, passing by the location of the food, withdrawing from the food, stopping on the way to the hiding location, or travelling in the opposite direction (see appendix to Chapter 4, Figure 4.3). The table also listed the reaction of the dominant—whether or not he followed, and on which trial. Most importantly, Coussi-Korbel listed the function and outcome of each of the actions: the subordinate attracted the dominant's attention elsewhere and withheld information about the food's location, and on those occasions, won the food.

Basic descriptive statistics are informative about broad behavioural patterns but an analysis of the consequences of winning or losing on a particular trial does not help describe the interaction that occurred leading up to that outcome. While the table and the text are very informative of the chronology and contingency of each subject's behaviour, the statistics in the results section are very simple: the percent of time the dominant followed the subordinate, the percent of time the subordinate went directly to the food, and the percentage of food won by each subject. These statistics do not show the more complex interactions, such as the percent of time the subordinate's tactics were successful or whether a particular tactic was more successful than another. Coussi-Korbel's descriptive statistics are not helpful in achieving the level of detail that would be required to demonstrate more subtle interactions, such as how gaze cues reveal information between subjects.

D. Hirata and Matsuzawa's (2001) analysis

Hirata and Matsuzawa (2001) provided a very rich description of how their chimpanzee subjects behaved in the experiment, including the details and timing of important interactions, and also a comprehensive table compiling both subjects' behaviour, trial by trial.

The table from Hirata and Matsuzawa (2001) is a great advance in describing the interaction appropriately (see appendix to Chapter 4, Figure 4.4). It provides sufficient information regarding not only the behaviour recorded for individual trials, such as each

subject's "degree of taking the optimal route" to the reward, whether they adjusted their direction, waited, and the frequency of looking towards the competitor, but it also shows changes in behaviour over the course of the interaction: there was a general increase in frequency of each behaviour as the chimpanzees competed to find the food, most notably in "misleading behaviour" (Hirata & Matsuzawa, 2001, p. 287).

While their table is informative, it lacks information about *which* particular behaviour in the dominant affected the informed individual. The reader can see on which trials the dominant adjusted her direction, but not whether that influenced the competitor to adjust *her* direction, or in which direction either individual moved, e.g., towards or away from the bait. Their table summarizes the broader patterns of the interaction but only the textual description reveals how the dominant's behaviour influenced the subordinate.

E. Held, Mendl, Devereux, and Byrne's (2002) analysis

Held et al. (2002) approached this problem by using logistic regression to find out whether the behaviour of a subordinate domestic pig was contingent on the exploitative behaviour of a dominant conspecific competitor. This analysis asked which factors influenced a subordinate individual's decision at certain points, defined by the authors as obvious foraging decisions, such as changing direction of movement (away from or towards the baited bucket), or approaching a food bucket (baited or unbaited). The subordinates' behavioural decisions were based on additive effects of several variables, different for each pair of competitors, including the (1) proximity between pigs, (2) the dominant's distance to food relative to the subordinate, (3) the dominant's direction of movement, and (4) whether the pigs could see each other during foraging. As well as giving a more detailed picture of the relationship between the informed pig's foraging decisions and the dominant pig's behaviour at specific moments, the logistic regression analysis also showed that subordinates predictably changed their behaviour when the dominants exerted a strong exploitation pressure during foraging (in that they were able to displace the subordinate pigs at the feeding bucket). Specifically, the subordinate pig avoided meeting the dominant at the baited food bucket.

1. Reasons logistic regression was not used in my analysis

A logistic regression appeared to be an appropriate candidate statistic for analysing data from my current study (as per Held et al., 2002), but on closer inspection, the data violated several assumptions of the test. Because a main focus of the current study is gaze

interactions, which tend to occur on a shorter time scale than other behaviour (locomotion, approaching a food location), data were entered into Microsoft Excel (2008) on a one-second time scale. Gaze therefore could not be compared to other behaviour such as locomotion, because those data were not independent: an individual walking continuously for 12 seconds did not walk 12 different times, whereas she could alternate her gaze 12 times. Furthermore, several predictor variables were highly collinear: for example, picking up the food necessitates that one individual is closer to it than the other.

Data could have been transformed to meet the assumptions of the test, as in Held et al. (2002) but this is an infeasible process: given the number of second-by-second observations per trial (some trials lasting several minutes), of 56 trials (24 *Competition*, 4 *No Knowledge*, 4 *Full Knowledge*, 4 *No Bait, No Knowledge*, 20 *Unequal Rewards*), for two chimpanzee pairs with 26 different behavioural categories, it would be beyond reason to transform all the data.

A more serious problem is that the data were coded in relative terms: ‘gaze towards bait’ is one specific direction, but ‘gaze away’ is every other direction *except* towards. Is there something inherently different about gazing towards the bait that would be a usable cue to the ignorant competitor, or is she following the informed subordinate’s gaze in *every* direction? To determine whether the dominant follows the subordinate’s gaze in every direction leads to another problem with the data coded in relative terms: if the subordinate is looking ‘right’ and the dominant is looking ‘right,’ are they looking to the same location? They are, only if they are both facing the same direction at the same time (as opposed to facing each other, for example). To account for this problem, data had to be re-coded in absolute terms: gaze towards quadrants 1, 2, 3, and 4. Even after this re-coding, it was determined that gaze to left or right could not be used in the analysis, because I had not coded body orientation *per se*, but instead I coded current location and direction of movement (this is a proxy for body orientation while a subject is moving, but when a subject is stationary, her body orientation was not coded); therefore, the problem of whether both chimpanzees were looking at the same place when both were coded as looking to the ‘right’ remained in the instance that at least one individual was not moving, whereas gaze towards one specific quadrant was valid without any movement cue.

F. Preuschoft's (1992) analysis

Instead of using a logistic regression, the pre-post- event histogram offered clear advantages. It allows the researcher to explore different variables and discover exactly which factors are significant in the model, rather than choosing *a priori* which variables were believed to have an influence before the analysis, as was done by Held et al. (2002). Employing a discovery method for the current study is useful, because I am specifically analysing gaze behaviour, which has not been analysed in depth before within this context, so it is unclear which factor or combinations of factors will have a significant influence on each subject's behaviour.

A study published on Barbary macaque facial expressions (Preuschoft, 1992) investigated whether the actions of one individual caused a reaction from a second individual. In the analysis, Preuschoft used a pre-post- event histogram (PPEH, Douglas & Tweed, 1979; Douglas & Sudd, 1980) to show the contingency relationship between the two individuals' behaviour. Preuschoft plotted the frequency of aggressive behaviour by animal B during the three minutes prior to and the three minutes following a silent bared-teeth display from animal A, in intervals of 10 seconds. She found that A's silent bared-teeth display reduced the frequency of aggressive behaviour in individual B, thus serving as a submissive behaviour. It is this type of time-locked analysis, the pre-post-event histogram, which has the potential to discern causal relationships during continuous interaction.

1. Exploring the PPEH method with my data

Analysis using pre-post- event histograms allows the researcher to define a specific, *referent* behaviour in one individual and determine how that affects a *target* behaviour in another individual. This method can be used with the data from my study to show how the actions of either chimpanzee subject affect certain behaviour in the other.

To create a histogram using the PPEH method of analysis, a referent behaviour was designated at time zero along the x-axis, and in the example below (using my data) the referent is the informed subordinate gazing towards the bait; and then the frequency or probability of a target behaviour, such as the ignorant dominant also gazing towards the bait, was plotted for every time t relative to the referent behaviour (Douglas & Tweed, 1979). The histogram plots the frequency distribution of the target relative to the referent, with time before zero representing target events that happened before the referent behaviour, and time after zero representing events occurring after the referent behaviour (Douglas & Sudd, 1980).

It is necessary to match all cases of the dominant's action with the event of the subordinate gazing towards the bait, each time it happens. Then, all cases of the subordinate's referent behaviour are aligned at time= 0, and the probability of the dominant's target behaviour is plotted, time-locked to the event.

I used the PPEH to analyse an example of gaze following, using data from my study: the informed subordinate Missy gazes towards the bait, and then the ignorant dominant Rita also gazes towards the bait, giving the appearance of 'gaze following.' Figure 4.1 shows a plot of the time series of the subordinate gazing towards the bait along the x-axis (each recording of the subordinate's gaze towards the bait is recalibrated at time= 0), and the probability of the dominant gazing towards the bait is plotted along the y-axis. The dispersion around the line represents one standard deviation from the binomial probability calculated for each point in time. Since the referent behaviour of the subordinate always occurs at time=0, the probability of the dominant's target behaviour can be compared during the time before and after the referent event, therefore showing the change in the dominant's behaviour as a function of the subordinate's behaviour. The graph shows that within the 20 seconds of the subordinate looking towards the bait, the probability of the dominant gazing in that direction nearly doubles, compared to the 20 seconds prior to the start of the subordinate's gaze. Furthermore, it is noteworthy that the probability that the dominant gazed towards the bait is very low *before* the subordinate gazed, showing that the dominant's target behaviour, gazing towards the bait, is contingent on the subordinate first looking towards it (this is the referent at time= 0).

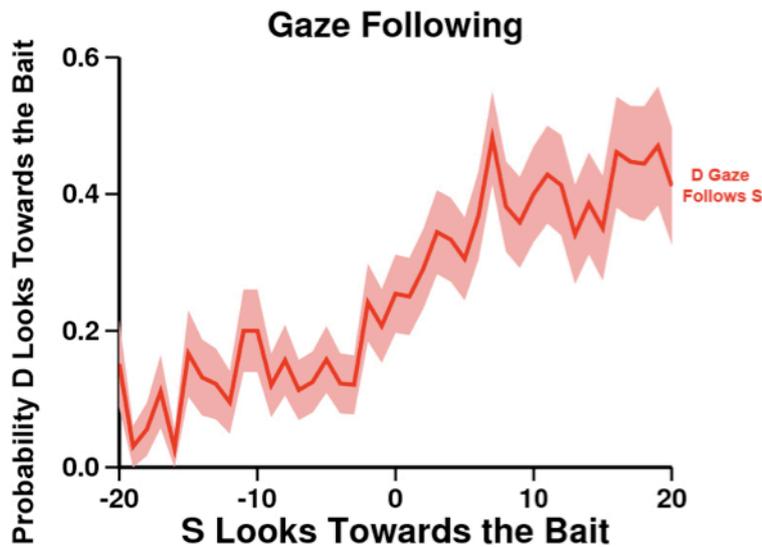


FIGURE 4.1: A pre-post- event histogram showing the probability of the dominant (D) gazing towards the bait (on the y axis) given that the subordinate (S) gazes towards the bait at time= 0 (on the x axis), Pair 1 Missy and Rita

This statistical method is therefore useful for demonstrating which behaviour in one individual affects another behaviour in the other subject: it is possible to compare for example, how the dominant's following affects the subordinate's decision to change her direction; or conversely, whether a subordinate's change in direction influences the dominant to follow. When considering the problem of describing the interaction at an appropriate level of detail, this method encompasses various solutions reached by other methods: it compactly describes statistical patterns at a comprehensive, time-locked level (in that the method consolidates many trials and shows that one subject's behaviour is conditional on another's and always occurs in the same time frame), and also allows the researcher to pull apart which variables have an effect, including additive effects, similar to the logistic regression used by Held et al. (2002).

2. Problems with PPEH analysis for my study

Making a statistical comparison pre- and post-event is, however, not straightforward, because if the subject exhibited the same pattern of behaviour on every trial, with or without an opponent, a time-locked graph comparing both chimpanzees' behaviour would imply a relation, but we would not know the source of the relation. For example, if the chimpanzees always turn left around an obstacle in their enclosure, and one arrives at the obstacle before the other, it would appear that the second in line is 'following,' even though she would turn

there had she been alone; her turn is not contingent on the other's turn. Or, as in the gaze following example above, if the subordinate gazes towards the bait for the entire trial, then comparing whether the dominant gazes towards the bait may make it seem as if the dominant's gaze is contingent on the subordinate's, when it may actually happen without relation to the subordinate's gaze direction.

Furthermore, with the PPEH method it is not possible to analyse behaviour when it does not happen. For example, if the subordinate attempts to withhold information, and does not gaze towards the bait, her behaviour would not be differentiated from other bouts of not looking towards the bait, and in fact cannot be analysed at all. Since understanding the interactions that lead up to episodes of withholding are important to the study of tactical deception, it is critical that an action can be analysed both when it occurs and also when it does not.

Instead of using a pre-post- event histogram, Dr. Mike Oram in the School of Psychology at the University of St Andrews suggested a different method: cross correlations. Both the logistic regression and the PPEH initially appeared promising, but a more sophisticated statistical technique is evidently necessary to show that each subject's behaviour is contingent on the other's and that their actions and interactions change over time. Basic descriptive statistics indicating which subject obtained the bait on each trial per condition, the pattern of food retrieval, and the average time to reward per condition, as well as a narrative describing the interactions, are presented at the beginning of Chapter 5: Movement Following. It should be apparent that one cannot rely on impressions from the narrative alone to conclude that, for example, the dominant's movement towards the bait was contingent on the subordinate first walking towards the bait. Nor can these descriptive statistics portray the interactions as often described in the text, much less the detailed gaze interactions (see Chapter 6: Gaze Following). Cross correlations capture the best features of both the logistic regression and the PPEH (i.e., shows time-locked contingent interactions, uses an exploratory method, etc.), while being overall less cumbersome and with fewer caveats to the interpretations. In the next section I describe how cross correlations are computed, how the correlogram graphs are constructed and tested for significance, in order to show the process through which my study was adapted for the statistic.

IV. An elegant solution: cross correlations

A. Data Structure

Based on results from previous studies (Menzel, 1974; Coussi-Korbel, 1994; Hirata & Matsuzawa, 2001; Held et al., 2002; Bugnyar & Kotrschal, 2004), I expected that the subordinate would find the banana unimpeded during the first few trials until the dominant adopted a tactic to obtain the food (e.g., following and/or taking the food). At this point, the subordinate would develop a counter-tactic (e.g., delaying approaching the food). In order to capture this progression, I split the data sets into three distinct phases, which were defined based on changes in the chimpanzees' behaviour, and were different for each pair (Held et al., 2002; Bugnyar & Kotrschal, 2004).

For Pair 1, subordinate Missy and dominant Rita, Phase 1 comprised those trials (1-7) in which the subordinate approached the food directly, and the dominant did not search for the food nor exploit the subordinate's success. Phase 2 (trials 8-12) was defined by the subordinate going directly to the location of the hidden food, and the dominant searching for the food while paying close attention to the subordinate. Finally, I defined Phase 3 (trials 13-24) by the subordinate avoiding walking directly towards the bait on many trials, and the dominant continuing her search.

For Pair 2, subordinate Reinette and dominant Georgia, Phase 1 (trials 1-11) was characterised by the dominant searching and the subordinate avoiding walking directly to the bait. I defined Phase 2 (trials 12-16) by the subordinate walking or running directly to the bait, and the dominant not following her. Phase 3 (trials 17-24) was defined by the subordinate alternating tactics between walking directly and delaying her approach to the location of the hidden food.

Data were re-coded in *absolute* terms (i.e., towards Quadrant 1, 2, 3, 4) to accommodate the problems associated with data coded in *relative* terms (e.g., towards/away from the bait); namely, to determine whether movement following and gaze following behaviour were due to some inherent cue relative to the bait (e.g., an olfactory cue), but not to other locations in the enclosure. Thus, the chimpanzees' enclosure was considered to comprise four approximately equally sized quadrants, each containing four hiding places for food. Rather than walking towards/away from the bait, or closer to/away from the other chimpanzee, locomotion data was split into three categories: (i) which quadrant of the enclosure the subject was currently in, (ii) which quadrant she was walking towards, and (iii)

whether there was a food item hidden in that direction. With these absolute codes it was easier to compare whether the dominant followed the subordinate when she moved in any direction, or only when she was moving towards the bait.

Standard statistical testing, Chi square goodness of fit tests and Analysis of Variance tests, were done in Chapter 5 to show general patterns of movement to each of the four quadrants.

B. How the cross correlation is computed

In neurophysiology, cross correlations are commonly used to report the relationship of firing rate between two neurons, a reference neuron and a target neuron that both produce information series called spike trains (Aertsen et al., 1989). Dr. Mike Oram has adapted this method for the purpose of this study: rather than comparing the relationship between two neurons, Dr. Oram guided me in using cross correlations to compare the behaviour of two chimpanzees. Each chimpanzee's behaviour was measured over a period of time, and each individual's actions were compared to those of the other individual, so as to determine whether the target chimpanzee's actions were contingent on, or occurred in a time-locked pattern relative to, the actions of the referent chimpanzee.

With cross correlations, a graphical output called a correlogram was constructed for each pair of variables tested. Similar to the pre-post- event histogram, cross correlations compare a referent behaviour at time= 0 in one individual's behaviour (in the PPEH example above, and in the cross correlation example using my data further below, the referent is the subordinate gazing towards the bait) with a target behaviour performed by another (the dominant also gazing towards the bait). A cross correlation measures the similarity of alignment and timing between two information series, and the correlogram plots the degree to which the two series are correlated in time, ranging from -1 (negative correlation) to +1 (positive correlation). Unlike the pre-post- event histogram, which shows the frequency or probability, a correlation measure of the referent behaviour with the target behaviour captures the occurrence of mutually inclusive events as well as the inverse, i.e., the non-occurrence of mutually inclusive events. All combinations of when the two behaviours do and do not happen are therefore taken into account.

My analysis used cross correlations in a discovery method to determine which behavioural variables, or combinations of variables, of one individual influenced the behaviour of the other. The process of the analysis correlated each variable with every other

variable, to compute all permutations. Rather than determining *a priori* which variables to test based on a theoretical assumption about their relationships, it was possible to sift through the permutations in an exploratory manner to determine those variables that were highly correlated.

C. Constructing a correlogram

For each of the chimpanzee interactions examined in this study, one subject's action was analysed for any potential influence on the other's; then the reverse analysis was conducted in order to compare both chimpanzees' tactics, as a control for the direction of the relationship. For instance, first the subordinate competitor's action was the referent against which the dominant's target action was compared; and then, for comparison, another correlogram was created using the dominant's action as the referent with which the subordinate's target action was compared.

The diagrams below (Figures 4.2-4.4) depict how a correlogram is created using neuron spike trains, since that is the original application of the method; one can imagine that for my analysis, each neuron is equivalent to a chimpanzee subject, and each spike in the neuron train is equivalent to each instance of a specific (target or referent) action that a chimpanzee performs. A referent neuron (or behavioural variable from one subject's dataset, e.g., gazing towards the bait) is chosen. The beginning of the time series of the referent is centred on time= 0 along the x-axis. For each performance of the referent behaviour (referred to as a "spike" in the diagrams below, recall that stimulated neurons produce information series called spike trains when firing), a small window is centred on it, and divided into sections called time bins. Then, a time series of the target neuron (or target behaviour from the other subject, e.g., also gazing towards the bait) is divided into time-bins and aligned with the referent's time series (Figure 4.2).

Once the time series are aligned, each time bin is filled with one count for each instance of the referent and the target behaviour happening; if both behaviours happen, one count is entered into the time bin for each (Figure 4.3). Finally, this process is repeated for each instance of the referent behaviour, as the second instance (or spike) becomes the new start of the time series, then the third instance, and so on (Figure 4.4) (Aertsen et al., 1989; Kumar, 2006).

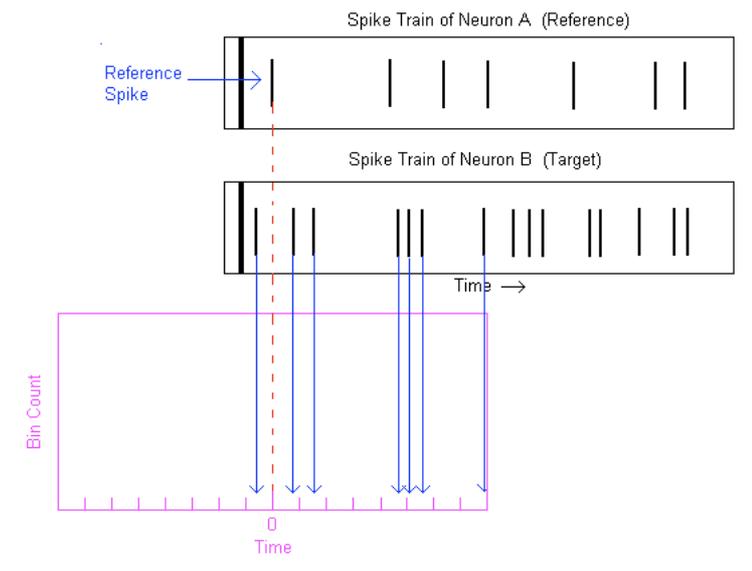


FIGURE 4.2: Aligning time series of referent and target behaviour along time bins (Kumar, 2006).

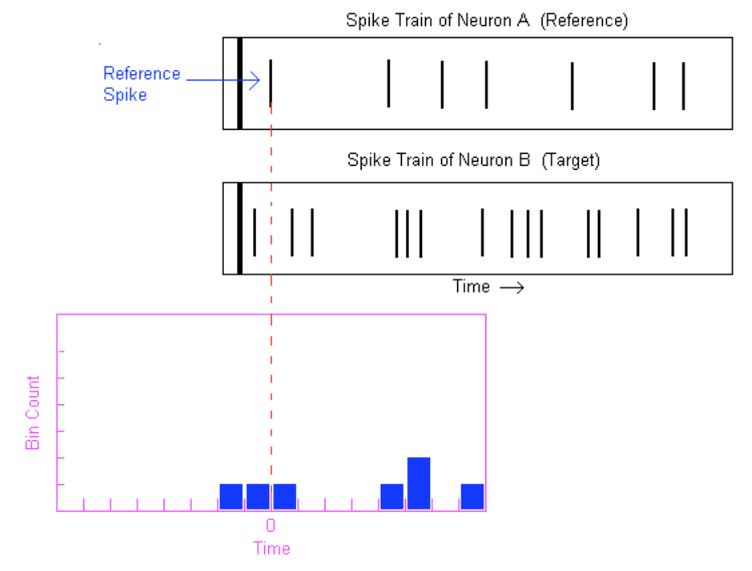


FIGURE 4.3: Filling time bins with appropriate counts of spikes (one for each time series) (Kumar, 2006).

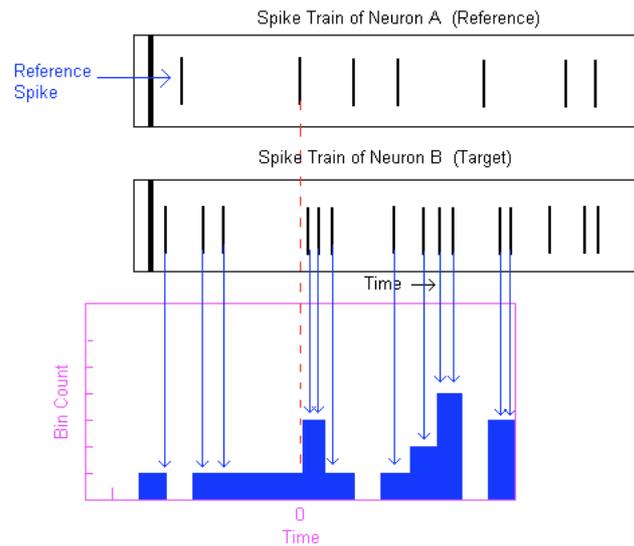


FIGURE 4.4: Repeat the procedure for the next reference spike, and so on (Kumar, 2006).

The correlogram plots the behaviour of the target with a time delay relative to the referent; the delay is measured along the x-axis both before and after time=0 (Aertsen, 1989). The correlation coefficient values are plotted, indicating the relationship of both individuals performing the behaviours (and conversely both not performing the behaviours).

For this study, I set the time range along the x-axis of the correlograms from 20 seconds before to 20 seconds after the referent event at time=0. This seemed like a reasonable time range in order to be able to show the relatively shorter time frame of gaze interactions, as well as the pattern of other actions such as movement following that occur over a longer time course. I did not suspect that a referent action would have a measurable effect on a target action more than 20 seconds after it happened, and in fact, often the data become sparse more than 20 seconds after a referent behaviour and are difficult to interpret (Aertsen et al., 1989). The correlogram shows the contingency between the two individuals' behaviour. Counts of the behaviour occurring after time=0 indicate that the target acted after the referent; on the other hand, counts before time=0 mean that the target acted before the referent. If there is no relation, one would expect the correlogram to be a flat line, since each particular time bin around the reference behaviour is no more likely to have a higher count of the target behaviour than any other time bin (Kirkland, 2006).

D. Creating a baseline for comparison

For the purposes of this analysis, in order to test whether a dependent relationship between the behaviour of two individuals really exists (as in the gaze following example), a baseline was created from the two variables being tested (referent and target). No data set, nor any theoretical numerical level of ‘chance’ association between behaviour of two chimpanzees in the same enclosure, exists against which to compare these data. Therefore, cross correlation data are compared to two baselines.

Within-trial and between-trial baselines were created using the original data points, but removing any time-locked relationships. To create the baselines, all of the data points of the referent variable are randomly permuted 10,000 times (without repetition), as well as the data of the target variable; then the correlations of the means of permuted data points are plotted in a correlogram.

If relationships between data points exist, either through time (sequence of actions) or relative to the other individual (time-locked contingent actions), they are disrupted in this process. The baselines therefore represent the theoretical distribution of the probability of a relationship, where there should be no relationship at all. Because the process of permuting the data points, or shuffling them, removes the time-lock aspect as well as the sequence of events, a pre-post- event comparison is no longer necessary, as in the PPEH approach.

Cases in which the original data line rises above or below the standard deviation of the means spread around a baseline for several seconds indicate that the correlation may be significantly different from the baseline, and therefore a relationship between those two tested variables exists. However, if the subjects behave in the exact same manner on every trial, with or without their opponent present, the shuffled baselines would have the same correlations as the data line, and would show no difference in behaviour.

1. Between-trial shuffled control

To create the between-trial shuffled control, the time series of a referent variable in trial 1 was permuted with the time series of the target variable from trials 2, 3, 4, etc., for each time either behaviour happened and each time either did not happen. The “Between” line, as seen in green on the correlograms throughout this dissertation, represents the correlations of the means of all the permutations. This mean, which may be skewed due to small sample size, is stabilised using a Fisher transformation; this allowed me to empirically construct the confidence intervals for the true value of the correlation. The Fisher

transformation re-samples the means of the correlations and computes the correlation of the re-sampled set, then transforms that value (using this formula: $0.5 \ln(1 + \text{re-sampled correlation}) / (1 - \text{re-sampled correlation})$). The new distribution is closer to being normally distributed, allowing me to construct confidence intervals for the new distribution. Then, these confidence intervals must be transformed back, in order to place them back into the range from which the original correlation coefficient was taken (Sokal & Rohlf, 1995; Hamrick, 2011).

In the figures that follow, the dispersion around the lines is from the values of the standard errors of the different permutations. The Between line is based on all the same data points as the original data line; it maintains the autocorrelations (the cross correlation of the referent behaviour with itself, which always peaks at time= 0) and directly accounts for the autocorrelation by asking whether the competitor's action is contingent on the referent *at the same time* (e.g., if the subordinate gazes towards the bait for the entire trial, and the dominant glances a few times, is that a contingent relationship?) The between-trial shuffled control maintains the sequential structure within each trial, but disrupts any potential relationships between trials relative to the start-time of each trial and any time-locked contingent relationships that exist between the two chimpanzee subjects.

2. Within-trial shuffled control

To create the within-trial shuffled control, the time series of a referent variable is permuted within each trial (10,000 random permutations), and the means of the permutations are correlated with the means of the permutations of the within-trial permuted time series of the target variable. The "Within" line (as seen in blue on the correlograms throughout this dissertation) represents the correlation of the means of all permutations (with Fisher transformations); the dispersion around the line is from the values of the standard errors of the different permutations. The within-trial shuffled control destroys the shape and structure of the autocorrelation, but maintains the overall number of data points within the autocorrelation, thus accounting for trials in which there is a lot of action (running, walking, gazing, climbing, searching) and trials in which nothing occurs (sitting, not searching): e.g., if one subject performs a particular behaviour for several seconds, the autocorrelation indicates the likelihood she will continue to do it 1, 2, 3, seconds later. The within-trial shuffled control maintains the frequencies of actions within a trial, but not their sequence, thus disrupting any correlation in time that two actions may have.

3. Summary

Two baselines were created by shuffling data both between and within trials, which represent the theoretical distribution of the probability of a relationship arising by chance, against which the correlation data are compared. The Between and Within lines on the correlograms represent the correlations of the means of all permutations with Fisher transformations; the variance around the lines is the standard error of the mean from the values of the different permutations. The Between shuffle disrupts time-locked contingent relationships between the subjects, and the Within shuffle disrupts the sequences of actions.

Data coded in absolute terms (i.e., towards quadrants 1, 2, 3, 4) are compared to the Between-trial shuffle: the chimpanzees were in a differently numbered quadrant on each trial, so shuffling between trials eliminated contingent relationships but maintained sequences of behavior (e.g., go outside and then turn left). Data that has been collapsed (e.g., “same quadrant” and “different quadrant”) are compared to the Within-trial shuffle: because the chimpanzees being together in a quadrant on trial one is not necessarily the same physical place as when they are together in a quadrant on trial two, a Within-trial shuffle is more appropriate because it maintains the contingencies but eliminates the sequences.

E. Significance testing with $-\log$ -likelihood values and t -tests

Cross correlation data are compared against the baselines of between- and within-trial shuffled data using a t -ratio. A t value of the observed data is calculated and compared with the means and standard errors of the shuffles with a t -test. The t -test determines whether the correlation coefficient is rare among the t sampling distribution, and is performed for each data point and its associated degrees of freedom. The resulting Significance Values graph (adjacent to correlograms throughout this dissertation) plots the negative logarithm values of the probability ($-\log$ -likelihood) that the t -test values exceed the critical value of $p=0.05$ at 2.9957 (hereafter rounded to 3.00) in the 40-second time frame around zero. If the data are significantly different from the between- or within-trial shuffled data, the lines on the Significance Values graph will rise above the red horizontal line at 3.00 that represents the 5% level of significance; any value plotted above that critical value is significant (larger absolute values are more statistically significant) (Aertsen et al., 1989), and therefore the y -axis on the Significance Values graph is truncated at 10.0 no matter the maximum plotted value to maintain consistency across all graphs.

V. Analysis of data from current study using cross correlation method

To demonstrate how the cross correlation works with data from the current study, I will continue with the example of gaze following. First, I will repeat the example shown above in Figure 4.1: when the subordinate gazes towards the bait, does the dominant gaze towards the bait? As shown below in Figure 4.5, after the subordinate gazed towards the bait, the dominant gazed towards the bait significantly more than expected from the within-trial shuffled control (collapsed data should be compared to the within-trial baseline). The correlogram on the left of each figure plots the cross correlation as well as the between- and within-trial shuffled controls. The Significance Values graph on the right of each figure plots the probability that the experimental data are different from the between- and within-trial shuffled controls.

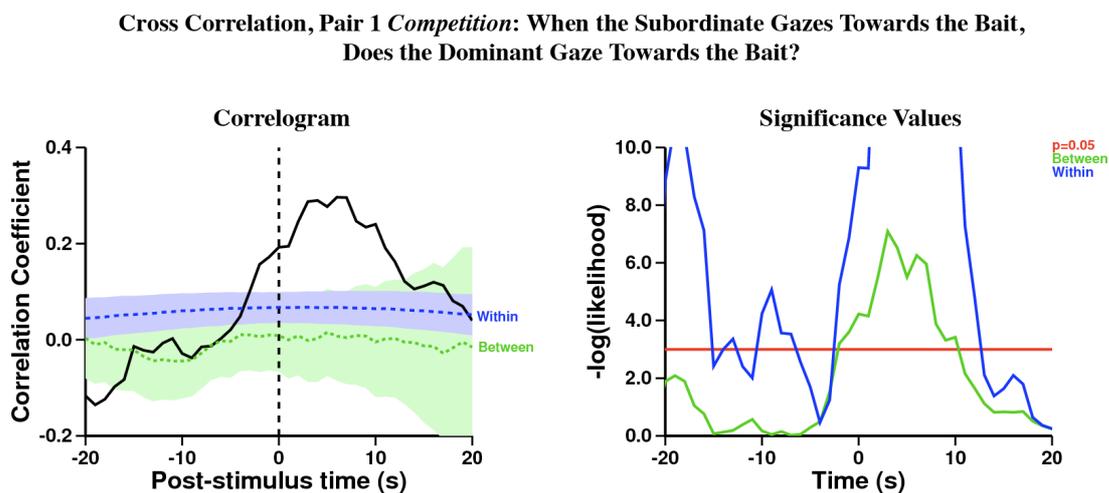


FIGURE 4.5: Referent behaviour: subordinate gazing towards the bait. Target behaviour: dominant gazing towards the bait. After the subordinate gazed towards the bait, the dominant gazed towards the bait significantly more than expected from the within-trial shuffled control (peak at time= +4, $r = 0.2897$, $n = 777$; $-\log\text{-likelihood} = 23.6418$, $p < 0.05$)

When the reverse situation is analysed (i.e., whether the subordinate looks towards the bait after the dominant starts looking towards it), it appears that the subordinate had already been gazing towards the bait by the time the dominant started to gaze at time= 0. The data in Figure 4.6 below are the same as in Figure 4.5 above: the cross correlation with the referent and target swapped results in a graph that is reversed in time along the x-axis.

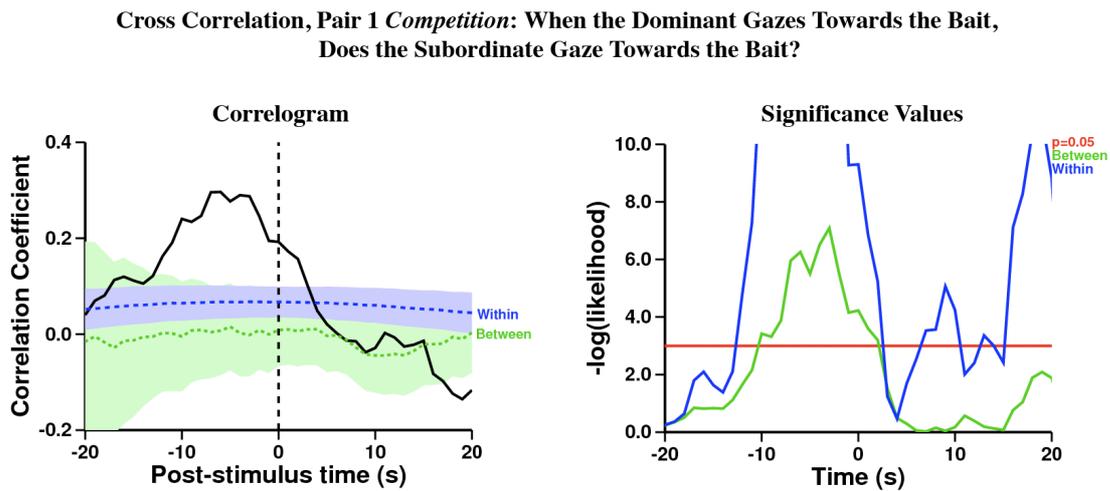


FIGURE 4.6: Referent behaviour: dominant gazing towards the bait. Target behaviour: subordinate gazing towards the bait. After the dominant gazed towards the bait at time= 0, the subordinate had already been gazing towards it significantly more than expected from the within-trial shuffled control.

The dominant followed the subordinate's gaze towards the bait; but did she follow gaze away from the bait? This is difficult to answer, since 'away' can be any other direction except 'towards,' and while both chimpanzees may be looking away from the bait, they might not be gazing towards the same place. This is exactly why I need to use absolute data, in addition. Thus, I analysed gaze following towards the four absolute quadrants of the enclosure. Figures 4.7-4.10 cross-correlate the referent behaviour at time= 0 of the subordinate gazing towards Quadrant 1 with the target behaviour of the dominant gazing towards quadrants 1, 2, 3, and 4; each cross correlation is represented in its own graph.

Figure 4.7 shows the cross correlation of the subordinate and the dominant both gazing towards Quadrant 1: after the subordinate gazed towards Quadrant 1 (and after she did *not* gaze), the dominant also gazed (and did *not* gaze), and this relationship is significantly different from the between-trial shuffled control (absolute data should be compared to the between-trial baseline). It appears that the dominant's gaze direction is contingent on the subordinate's direction of gaze.

**Cross Correlation, Pair 1 Competition: When the Subordinate Gazes Towards Quadrant 1,
Does the Dominant Gaze Towards Quadrant 1?**

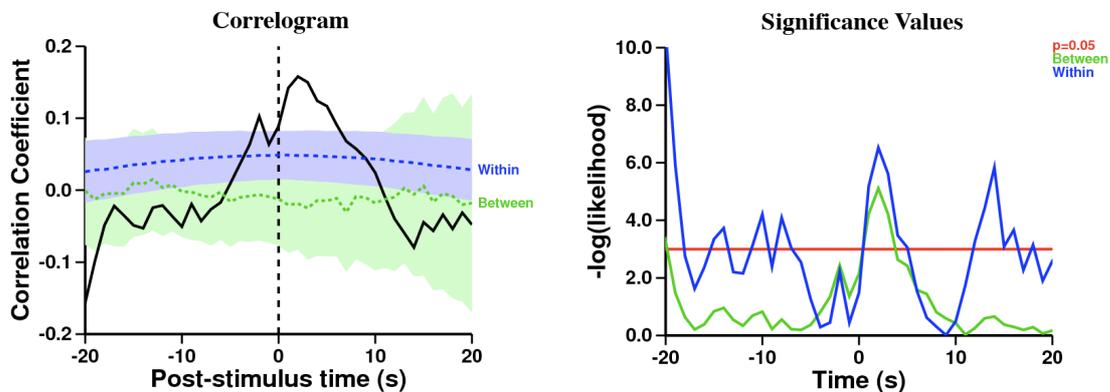


FIGURE 4.7: Referent behaviour: subordinate gazing towards Quadrant 1. Target behaviour: dominant gazing towards Quadrant 1. After the subordinate gazed towards Quadrant 1, the dominant gazed towards Quadrant 1 significantly more than expected from the between-trial shuffled control (peak at time= +2, $r= 0.1420$, $n= 843$; $-\log\text{-likelihood}= 5.1116$, $p<0.05$)

The graphs in Figures 4.8-4.10 below show the value of this method of analysis: when the subordinate was gazing towards Quadrant 1, the correlation coefficient of the dominant gazing towards Quadrant 2, 3, or 4 is low and not significantly different from the between-trial shuffled control.

**Cross Correlation, Pair 1 Competition: When the Subordinate Gazes Towards Quadrant 1,
Does the Dominant Gaze Towards Quadrant 2?**

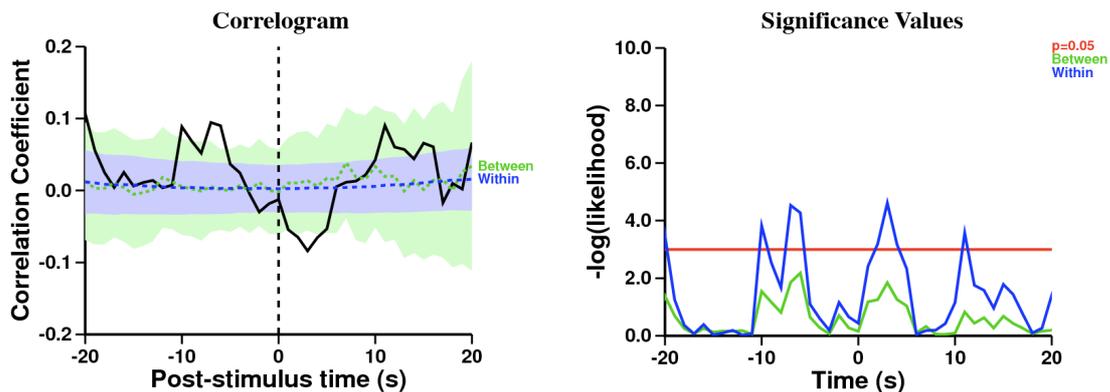


FIGURE 4.8: Referent behaviour: subordinate gazing towards Quadrant 1. Target behaviour: dominant gazing towards Quadrant 2. After the subordinate gazed towards Quadrant 1, there is no relation of the dominant gazing towards Quadrant 2 compared to the between-trial shuffled control.

Cross Correlation, Pair 1 *Competition*: When the Subordinate Gazes Towards Quadrant 1, Does the Dominant Gaze Towards Quadrant 3?

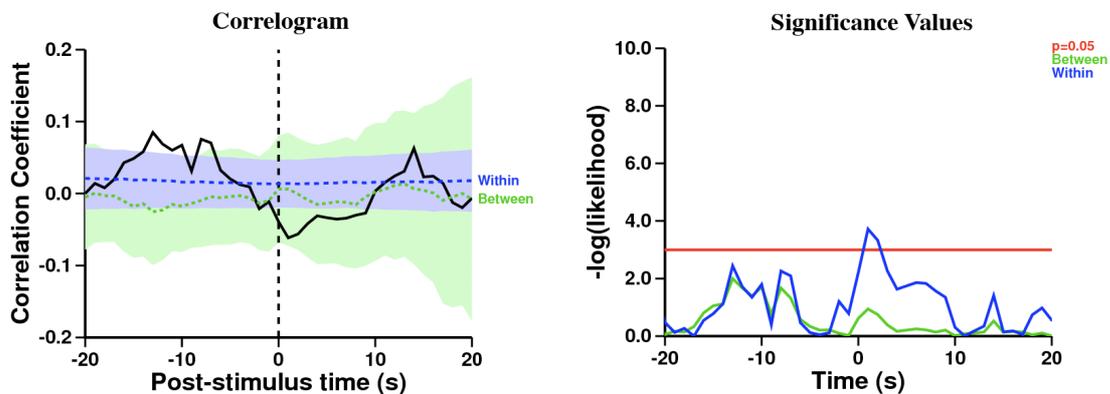


FIGURE 4.9: Referent behaviour: subordinate gazing towards Quadrant 1. Target behaviour: dominant gazing towards Quadrant 3. After the subordinate gazed towards Quadrant 1, there is no relation of the dominant gazing towards Quadrant 3 compared to the between-trial shuffled control.

Cross Correlation, Pair 1 *Competition*: When the Subordinate Gazes Towards Quadrant 1, Does the Dominant Gaze Towards Quadrant 4?

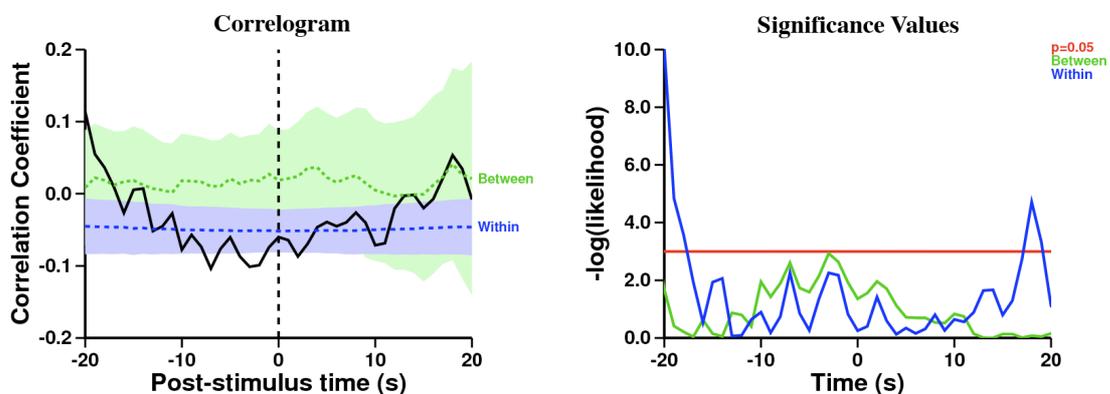


FIGURE 4.10: Referent behaviour: subordinate gazing towards Quadrant 1. Target behaviour: dominant gazing towards Quadrant 4. After the subordinate gazed towards Quadrant 1, there is no relation of the dominant gazing towards Quadrant 4 compared to the between-trial shuffled control.

As expected, the between-trial shuffled controls on these graphs generally hover around zero: there is no relationship between points when the relative time-locked relationships are disrupted. Additionally, there seems to be no relationship between the two subjects' gaze behaviour towards incongruent quadrants. The graphs serve to demonstrate this intuitive lack of relationship, and the fact that there is a sustained correlation when both

subjects gazed towards Quadrant 1 emphasizes that both subjects were often gazing in the same direction. This pattern holds true for the subordinate gazing towards quadrants 2, 3, and 4: the dominant also gazed towards the same direction at a significantly high level, but not towards any other direction (see Chapter 6: Gaze Following). Therefore, the chimpanzees not only gaze towards the relative position *of the bait* at the same time, but *in general* after the subordinate starts to gaze towards a specific direction in the enclosure the dominant also gazes towards the same direction as the subordinate.

VI. Discussion

The cross correlation analysis describes the informed forager interaction at a very detailed level, demonstrating which relationships are contingent and in which directions; for example, the dominant follows the subordinate's gaze. On the other hand, using this method can also provide a description of the broader patterns of interaction; that, for example, dominants follow the subordinates' gaze in every direction, not only towards the bait. This allows one to ask probing questions such as, if dominants follow gaze in every direction, what is it about gazing towards the bait in particular that allows her to gain information about its location?

To summarize, the cross correlation method of analysis has many advantages. Correlations can be plotted along one-second intervals, and graphs can be narrowed down to a small range surrounding the desired interaction to show the time frame of changes in behaviour as well as the duration of an interaction.

Cross correlations show that one individual's behaviour is often contingent on her opponent's by correlating not only when both individuals perform the target action(s), but also when they both do not perform it. Therefore, this can demonstrate a relationship that other authors have indicated seems to exist, but their analyses cannot conclusively show.

A great benefit of the method is being able to select which variables to correlate in an exploratory manner. This way it is possible, similar to the Held et al. (2005) method, to show, for example, exactly which of the dominant's behavioural variables are correlated with the subordinate changing direction or approaching the food. Beyond this, the exploration can elucidate relationships where none were assumed to exist, or where one might not have thought to look.

The method of testing for statistical significance allows the researcher to create a baseline against which to compare the data, using the same data points in a randomly permuted order. This baseline is the theoretical distribution of the probability of a relationship appearing by chance.

Using the cross correlation analysis will provide the most detailed and most comprehensive look at how chimpanzees use “continuous feedback” (Menzel, 1974, p. 134) when monitoring their competitor’s behaviour. This is because it allows the researcher to show relationships that would either have remained undiscovered, or difficult to prove if they seemed to be present, even with a great deal of top-down analyses to pick apart using a logistic regression. It can be used to explore, statistically, what Menzel and others have described so well in text, and have attempted to show with varying degrees of success using maps, graphs, and tables.

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I. Abstract

Two pairs of chimpanzees competed in the informed forager paradigm, and due to the differences in their knowledge regarding the location of a hidden food item, the informed subordinate adopted the role of producer, and the ignorant dominant adopted the role of scrounger. The dominant followed the subordinate in order to exploit her foraging success; previous studies defined movement following in one way, which was insufficient to show the level of detail desired for this analysis. I used cross correlations to examine how each subject used three types of movement following: *approaching*; following in the other's *footsteps*; and *converging* on the other's destination. Data were divided into three phases based on changes in the subjects' behaviour; analyses were therefore able to show how movement patterns changed over the course of the experiment. In particular, I analysed how the dominant's distinct following tactics affected whether the subordinate avoided walking directly to the food reward; the subordinate's evasion tactics functioned to deceive the dominant. I also analysed how the dominant's tactics changed when the subordinate delayed her approach to the food. I showed that for both pairs, the dominant adjusted her movement to get physically closer to the subordinate more than the subordinate moved to be closer to the dominant. For Pair 1, the dominant Rita *approached* and followed in the subordinate Missy's *footsteps*, which immediately led to the subordinate pausing her movement. For Pair 2, the correlograms for *footsteps* behaviour indicate that each chimpanzee was 'taking turns' following her opponent: the dominant Georgia followed, then ran ahead of the subordinate ReINETTE, and finally the subordinate overtook the dominant to run to the reward. Using a new method of statistical analysis, cross correlation, will improve our understanding of the contingencies between both chimpanzees' actions as well as how each subject changes her behaviour over time. For the informed forager paradigm, behavioural evidence of conditional relationships can be interpreted in the context of what each subject knows about the other's knowledge. The results of this in-depth analysis speak to the importance of analysing data on a more detailed level (i.e., more specific definitions and dividing data into phases) in order to find and interpret behavioural patterns when they are most likely to occur.

II. Introduction

It has been proposed that primate cognition evolved to cope with the challenges of social living, such as exploitation during foraging (Chance & Mead, 1953; Humphrey, 1976;

Jolly, 1966; Kummer, 1967). Optimal foraging theory suggests that individual foragers should maximise food intake relative to time spent searching (among many other factors) (Emlen, 1966; MacArthur & Pianka, 1966). In the informed forager paradigm, one individual is given privileged knowledge of the location of a hidden food item, and is released into a foraging arena with an ignorant competitor (Menzel, 1974). Due to the difference in their knowledge, the two competitors must therefore adopt different tactics to find it, such as producer and scrounger strategies (Barnard & Sibly, 1981; Barnard, 1984). Individuals of higher rank can take advantage of the effort made to find food by lower rank individuals, and it is common for dominants to scrounge on subordinate producers by using social or physical pressure (Baker et al., 1981; Rohwer & Ewald, 1981; Caraco et al., 1989; Gross, 1996; Barta & Giraldeau, 1998; Ducoing & Thierry, 2003).

In previous studies using the informed forager paradigm, authors provided rich narrative descriptions of interactions between competitors, such as how informed subordinates acted to counter the dominant's exploitation by delaying their approach to the food, or by moving in a different direction (Menzel, 1974; Coussi-Korbel, 1994; Held et al., 2000, 2002, 2010; Hare et al., 2001, 2003; Hirata & Matsuzawa, 2001; Ducoing & Thierry, 2003, 2004; Bugnyar & Kotrschal, 2004; Schloegl et al., 2008b). These withholding and misleading manoeuvres can function as tactical deception (Menzel, 1974; Coussi-Korbel, 1994; Hirata & Matsuzawa, 2001; Held et al., 2002; Ducoing & Thierry, 2003). However, the question has been raised as to whether the subordinates' actions were intentional, in that they acted appropriately to reach a goal. Menzel (1974) wrote,

“The only way in which the question of intent can be assessed with animals is to examine how the leader's actions vary as a function of the consequences they produce in the actions of the followers. Locomotion and visual orientation, as well as tapping and some molecular signals, are clearly “intentional” by this criterion” (p. 134).

However, previous studies have had difficulty in showing statistically how each subject's tactics changed over time, and whether one subject's actions affected the actions of the other. Held et al. (2002) successfully showed that the subordinate's decision to retrieve the food was affected by whether the dominant was farther away from the food, moving away from the food, or not visible to the subordinate. The current study seeks to elaborate on this point using cross correlations. This chapter specifically analyses each subject's locomotion,

and the next chapter analyses their visual orientation, couched in an intentional stance and cognition framework (Byrne & Whiten, 1991; Byrne, 1997; Byrne & Bates, 2006).

The aim of the current experiment was to understand how an ignorant dominant chimpanzee exploits an informed subordinate's knowledge regarding a hidden banana, and whether the subordinate could avoid such exploitation. Previous studies have only defined movement following in one way, which was insufficient for the level of detail desired for this study (Leca et al., 2003; Meunier et al., 2008; Sueur & Petit, 2008, 2010; though see Stueckle & Zinner, 2008, for "leading from the back"). My analyses focused on each chimpanzee's movement through the enclosure—specifically, three types of following behaviour: follow by *approaching*; follow in the other's *footsteps*; and follow by *converging* on the other's destination. Furthermore, each subject used distinct types of following as the experiment progressed, and so data were divided and analysed in three different phases to show how tactics changed over time. Different following types varied with different states of knowledge in various control conditions. I examined how the dominant's distinct tactics affected the subordinate's decision whether to walk directly to the food reward or not, and subsequently how the dominant's tactics changed when the subordinate delayed her approach to the food. The cross correlation analysis allows me to show the behavioural contingencies that exist between two foraging subjects, as well as changes in their behaviour over time; results can be interpreted in the context of what each subject knows about the other's knowledge.

A. Follow by *Approaching*

In order for the dominant to exploit the subordinate's foraging success, a simple action she could take is to walk towards where the subordinate is currently located, whether or not the subordinate is currently moving. Thus the dominant would be tracking the subordinate's location and adjusting her own direction to *approach* her. Hirata and Matsuzawa reported their ignorant chimpanzee subject "gained access to the reward by keeping close to and frequently adjusting her direction to" the informed subordinate (Hirata & Matsuzawa, 2001, p. 290). I define follow by *approaching* as: "the subjects are in different quadrants of the enclosure and one individual moves (walks/runs/climbs) towards the other." This definition does not specify whether the other is also moving; sometimes the subordinate would sit near the food but delay picking it up, and the dominant *approached* her where she sat. Furthermore, it does not specify the other's direction of movement if/when she is moving: for example the dominant can *approach* the subordinate as the subordinate is

mutually *approaching*; in this case the dominant walks to where the subordinate is (and the subordinate walks to where the dominant is), but they are moving in different absolute directions. The subject does not need to cross into the other quadrant to be considered an *approach*. A constraint of this definition is that the two chimpanzees must be in different quadrants; when they are in the same quadrant and the dominant walks towards the subordinate, whether or not the subordinate is moving, is not covered by any of my following definitions.

B. Follow in the Other's *Footsteps*

Instead, when the chimpanzees are together in the same quadrant, a different kind of following is possible, in the sense of following in the other's *footsteps*. I define following in the *footsteps* as: "both subjects are in the same quadrant, and both moving towards the same (any) quadrant, and one individual is moving towards the other and the other is moving away from the first individual." This is the closest approximation using the coding scheme to saying that one chimpanzee follower is walking behind the other chimpanzee leader.

C. Follow by *Convergence*

The third sense in which one animal can follow another requires some perspective-taking ability: if one individual can take the perspective of the other and *converge* on her inferred destination, then the first individual may modify her own movement to arrive at the same destination. Hirata and Matsuzawa wrote of their chimpanzee subjects, "Pendesa began to approach Chloe's route from some distance away," (Hirata & Matsuzawa, 2001, p. 290) an interaction I attempt to capture with this definition: I define follow by *converging* as "the subjects are in different quadrants and moving towards the same (any) quadrant." Again, a practical constraint here is that this definition can only be applied when the two chimpanzees are in different quadrants; the definition no longer applies when they are in the same quadrant, though they may arrive at the same destination from different starting points within the same quadrant. Since this definition does not specify which chimpanzee walks first, or upon whose movement the direction of the other is contingent, the true 'follower' may be the animal in front (Stueckle & Zinner, 2008). The only specification is that both are in two different locations, and from those two locations they both direct their movement towards the same location.

These definitions are not mutually exclusive in all cases. For example, it could be conceived that the two chimpanzees are in different quadrants and the dominant is

approaching the subordinate; and if they are both moving towards the back corner of the quadrant that the subordinate is currently in, then the dominant is also *converging* on the subordinate's destination. Once the dominant enters the same quadrant as the subordinate, there is only one applicable definition, so in this example we can only detect if she is walking in the subordinate's *footsteps*.

This chapter examines how each chimpanzee moves in relation to the other by addressing each of the three definitions separately. For each type of following, I will present cross-correlograms and $-\log$ -likelihood graphs for the entire *Competition* dataset, which is then divided into the three phases of the trials, and then the *No Knowledge*, *Full Knowledge*, and *No Bait*, *No Knowledge* controls are presented.

III. Results: Pair 1, Missy and Rita

A narration of both subjects' behaviour will give the impression that the subordinate acted intentionally to mislead the dominant away from the hidden bait, and that on several trials the dominant gained some cue in the subordinate's behaviour, likely her movement towards and/or proximity to the bait, that allowed the dominant to find and scrounge the reward. However, though a description of what an observer sees may imply that the 'dominant *knows* that the subordinate *knows* where the banana is,' we cannot be sure without fully exploring the relationships in the data that may provide evidence to support the hypothesis that the dominant uses some physical movement cue from the subordinate to inform her own search for the hidden bait. The questions that will be addressed include: who found the reward? Did the dominant walk towards the bait after the subordinate walked towards the bait, and does this pattern extend to other areas of the enclosure? Did the dominant *approach* the subordinate, follow in her *footsteps*, and *converge* (and did the subordinate use these movement types to follow the dominant)?

A. Who Found the Reward?

The subordinate, Missy, was informed of the location of the hidden food in the *Competition* trials, and ultimately obtained 18 of 24 bananas (75%). Rita, the ignorant dominant, obtained the banana on the other six trials (25%) despite not knowing ahead of time where it was hidden, indicating that she represented a moderate level of exploitation pressure upon Missy. For comparison, when neither subject knew where the banana was hidden in the *No Knowledge* controls, the subordinate found the banana on one of four trials,

and neither chimpanzee found the bait on the remaining three trials. In the *Full Knowledge* condition, the dominant found two of four bananas, the subordinate found one, and neither chimpanzee picked up the banana on the fourth trial. No bananas were hidden in the *No Bait*, *No Knowledge* controls (Figure 5.1). From this initial glance at the overall percentage of food won by each subject, we have learned that when an individual had seen where a reward was hidden, she was more likely to find it than when she had not seen it hidden.

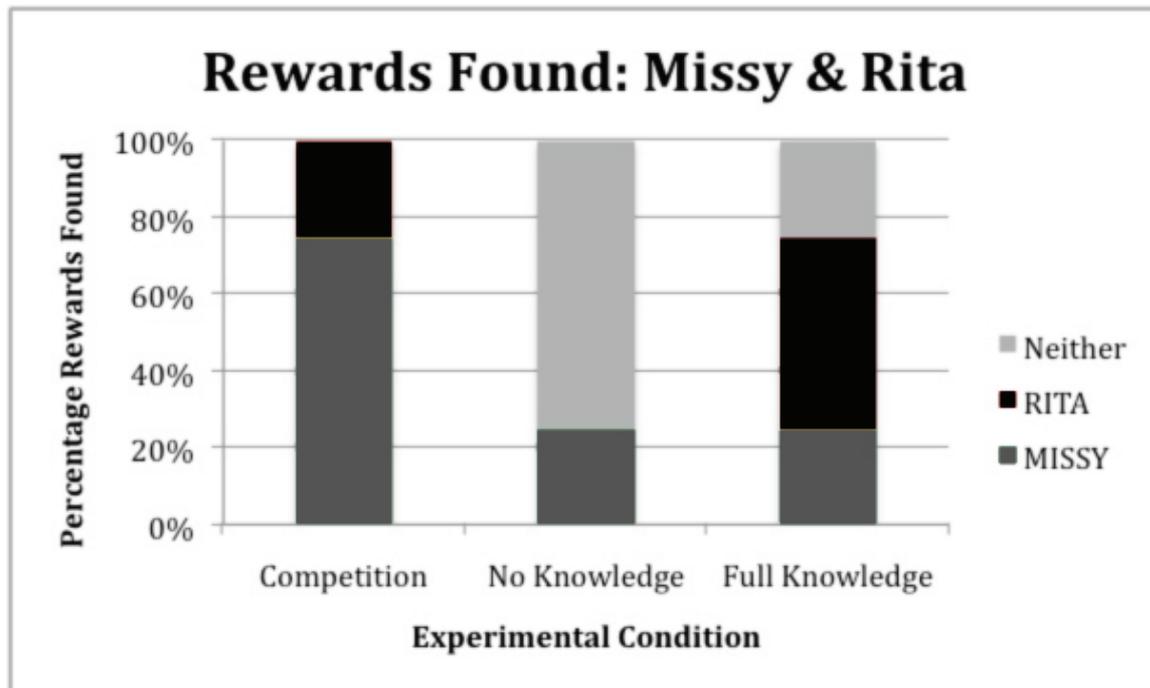


FIGURE 5.1: Percent rewards found by each subject, per condition, Pair 1

B. Descriptive Account of *Competition*

The pattern of reward retrieval is more telling of the progress of the interaction (Figure 5.2). The subordinate found the banana on the first ten trials, and then the dominant picked it up on trial 11. The subordinate retrieved the reward on the next three trials, and then the dominant also retrieved three in a row. The subordinate won on trial 21, then the dominant, then the subordinate, and on the last trial neither chimpanzee found the banana.

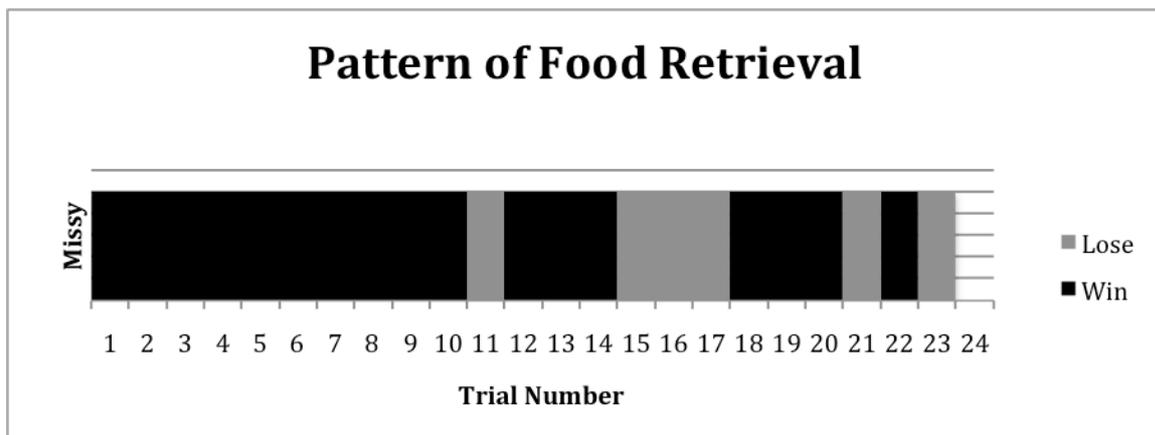


FIGURE 5.2: Pattern of the Subordinate's Food Retrieval, Pair 1

The dataset was divided into three phases based on changes in either partner's tactics. Phase 1 (trials 1-7) was defined by the subordinate walking directly to the reward, and the dominant did not exploit the subordinate. Phase 2 (trials 8-12) was defined by the dominant actively searching for the reward, though the subordinate continued to find it on most trials. Phase 3 (trials 13-24) was characterised by the subordinate delaying her approach to the food or taking an indirect path, while the dominant successfully gained the food reward on five trials.

Overall, the mean trial length for the *Competition* was 50.9 seconds (Figure 5.3). When no bait was found, the trial was terminated at 300 seconds (this affects the *No Knowledge*, and *No Bait, No Knowledge* conditions, as well as the final trial in Phase 3 of the *Competition* and one trial in the *Full Knowledge* condition). The mean trial length for the *No Knowledge* condition was 247 seconds, 95.5 seconds for *Full Knowledge*, and 300 seconds for *No Bait, No Knowledge*. An ANOVA tested the differences in mean trial time and found a significant difference between conditions ($F= 16.26$, $df= 39$, $p < 0.01$).

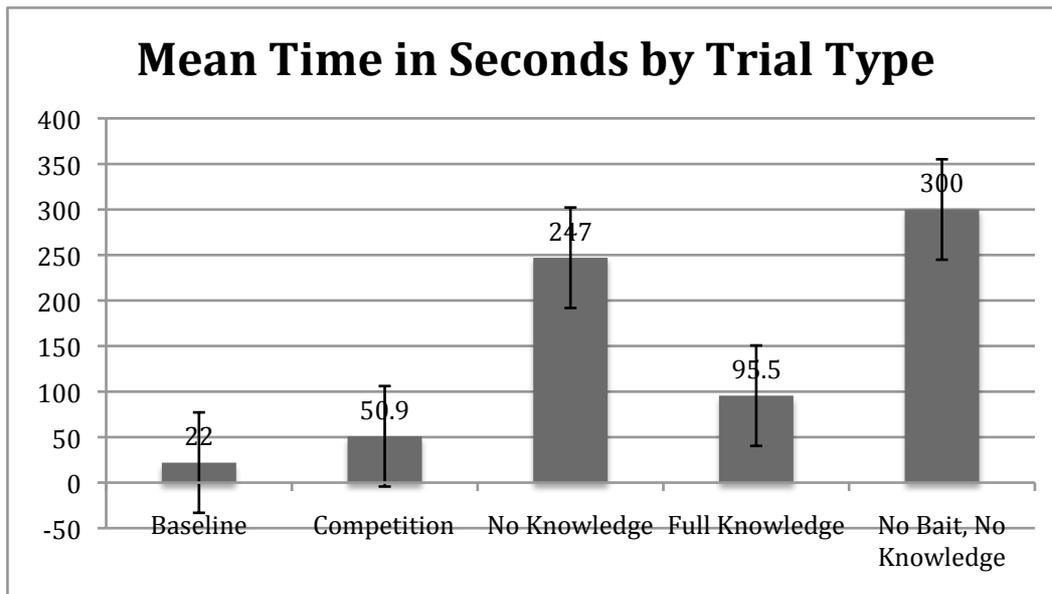


FIGURE 5.3: Mean trial time with standard error, per condition (no banana was hidden in the final *No Bait, No Knowledge* condition), Pair 1

As the dominant's movement and search tactics changed, so did the subordinate's; this is reflected in the mean trial time, which increased over the three phases as the subordinate avoided walking directly to the bait. The mean trial length during Phase 1 was 19.85 seconds; the mean trial length during Phase 2 was 28.6 seconds; the mean trial length in Phase 3 was 78.25 seconds. An ANOVA tested the differences in mean trial time and no significant difference was found between the phases ($F= 2.877$, $df= 23$, $p= 0.079$).

1. Phase 1: Trials 1-7

On the first three trials of the experiment, the knowledgeable subordinate walked straight to the reward without hesitation while the ignorant, naïve dominant did not seem to pay attention to her, and did not interact with her. By the fourth trial, the dominant started climbing onto the structure in the centre of the enclosure to watch the subordinate as she walked directly to the banana to pick it up, and the dominant did not interfere. On trial seven, the dominant was again watching the subordinate from her position on the climbing structure, and began to sway threateningly. The banana was hidden in a hanging tire suspended from the climbing structure, directly in front of where the dominant was standing. The subordinate picked up the banana and reciprocated the threatening behaviour by swinging the tire towards the dominant and then running away from her while fear grimacing. The interaction at the

hanging tire gave the impression that the dominant realised at this moment that the subordinate had information about the hidden banana.

2. Phase 2: Trials 8-12

For the first time on the eighth trial, the dominant immediately searched in the hanging tire where the banana had been hidden on the previous trial. When she did not find it there, the dominant walked towards the subordinate and followed her very closely, walking bipedally and threatening. On trial nine, the dominant searched again in the hanging tire. By trial ten, the dominant again walked towards the subordinate, and also walked towards the same place that the subordinate walked, but stopped short of arriving at the same location. On trial 11, the dominant watched as the subordinate found the banana, but after a moment's pause, the subordinate abandoned the reward and walked away, allowing the dominant to pick it up. The dominant continued to search on the subsequent trials as well as walk towards where the subordinate was walking, giving the appearance of following. As the dominant increased her threatening and following behaviour, the dominant was able to exploit the subordinate's foraging success. It appeared that the dominant was following the subordinate in order to exploit her.

3. Phase 3: Trials 13-24

Phase 3 was characterised by the subordinate adopting different tactics to avoid the dominant's exploitation, such as delaying her approach to the food or walking away from where the bait was hidden. On trial 13, before reaching the reward, the subordinate sat down and turned her back to it for 1:04 minutes, which functioned to withhold information from the dominant. The subordinate waited to pick up the food until the dominant ceased watching her and returned towards the start cages. On trial 14, the dominant was searching as the subordinate approached the reward; as the subordinate bent down to lift the red plastic ring in Q3 under which the banana was hidden, the dominant turned around and brusquely marched towards the subordinate. Acting quickly, the subordinate sat directly on top of the plastic ring for 13 seconds, preventing the dominant from looking under it. Then, the subordinate walked off towards the climbing structure, making frequent eye contact with the dominant, who followed closely. Both chimpanzees sat on the climbing structure for 33 seconds during which time the subordinate gave no indication that she was searching for a hidden food item, and then the dominant climbed down and walked away. The subordinate then returned to the red ring, first checking that the dominant was not watching her, and lifted it to find the

banana. At that moment, the dominant turned around to witness the subordinate picking up the reward. It appeared as if the subordinate ‘*thought* that the dominant *believed* that the subordinate *knew* where the food was hidden,’ and the subordinate appeared to take advantage of the dominant’s belief by first withholding, then misleading the dominant away from the bait. However, in previous observations of tactical deception, instances like this were seen as isolated events, possibly the culmination of several factors (e.g., learning, circumstance). It seems that a useful tool for analysis to determine which factors contribute to interactions such as this would compare all instances of changes in behaviour, and contingencies between competitors, to ask whether a pattern actually exists where an observer seems to think one does—or even where an observer might not think to look.

On trial 15, the dominant watched the subordinate closely, and once the subordinate had uncovered the reward, the dominant walked towards her and took the reward from her. On trial 16, the dominant saw the direction in which the subordinate was moving, and ran ahead of her to reach the reward first. On trial 17, the dominant again followed the subordinate; the subordinate arrived at the hiding location in Q1 but refrained from searching for the banana under the white barrel for 50 seconds. The dominant began to search elsewhere, and the subordinate uncovered the reward, but as on trial 11 in Phase 2, she walked away and let the dominant take the banana. The dominant continued to follow, threatened the subordinate, and ran ahead of her, but despite the intimidation and exploitation tactics, the subordinate obtained the banana on three consecutive trials (18, 19, 20).

4. *No Knowledge* controls

In the first *No Knowledge* control trial, the subordinate walked into the enclosure and happened to notice the banana in the culvert in Q1. She sat down with her back turned for 20 seconds as the dominant sat on the climbing structure and eventually climbed down to return inside, at which point the subordinate picked up the banana. The dominant came back outside and peered as the subordinate ate. On the second trial, both chimpanzees continued to search; the subordinate looked where she had found the reward on the previous trial, and then walked around the entire enclosure, searching in ten more places, and again returned to the culvert in Q1, without finding the hidden banana. On the third trial, the dominant stayed inside as the subordinate searched six locations before returning inside. On the last trial, the subordinate again searched in three places, including the culvert in Q1, and returned inside. The subordinate’s pattern of searching was very different from *Competition* trials in which she

had seen where the food was hidden: on those trials, she usually went straight to the reward, and if not by a direct path, she did not usually search in other locations nor search in the same place more than once.

5. Phase 3, continued

After the four *No Knowledge* control trials, the *Competition* resumed. On trial 21, the subordinate delayed approaching the reward for 30 seconds, then searched in the tire in Q1. After looking into the tire, she glanced at the dominant, who immediately walked up to the subordinate, and again the subordinate let the dominant take the banana. On trial 22, the dominant travelled across the enclosure towards the subordinate and then followed her closely to the reward. Though the dominant was only a few paces behind the subordinate and could have easily taken the reward, the subordinate arrived at the banana first and kept it. On trial 23, the dominant threatened the subordinate as she looked under the kegs where the banana was hidden. After looking, the subordinate walked away, perhaps in an effort to mislead the dominant or possibly to avoid conflict, and the dominant climbed down to the kegs, looked under, and found the banana. Neither chimpanzee retrieved the banana on the last trial. On many trials in Phase 3 it seemed that the dominant retrieved the banana because the subordinate revealed some cue to her, whether by physically sitting near the reward, actively searching for the reward, or glancing towards the dominant as soon as she had found the reward.

6. Full Knowledge controls

On the first two trials of the *Full Knowledge* controls, the dominant ran out of her cage in the 'Cognition Room' to the reward. On the third trial, the dominant stayed inside the 'Cognition Room' as the subordinate slowly and nervously approached the hiding location to retrieve the banana. On the final trial, only the subordinate came outside, and she sat on the central climbing structure without searching for the food. Though I expected the dominant to pick up the banana on every trial in this condition, she did not, and it could have been due to the dominant's lack of motivation to enter the enclosure on that particular day, to a conflict between the chimpanzees of which I was not aware, or to any number of factors that I cannot explain.

7. No Bait, No Knowledge controls

On the first trial of the *No Bait, No Knowledge* controls, the subordinate searched in six places and the dominant searched in three. On the second trial, the subordinate sat on the

climbing structure for the full trial without searching, and the dominant came outside for only 1:27 minutes and sat on the climbing structure as well before returning inside. Both chimpanzees stayed outside for the full third trial: the dominant sat on the climbing structure and the subordinate sat against the outer wall in Q1. On the final trial, the dominant came outside and searched in six locations, while the subordinate only came outside for the second half of the trial.

8. Summary

Over the course of the *Competition*, it appeared that a tactical arms race was developing between the two chimpanzees: first the subordinate walked to the reward and the dominant remained naïve to the experimental condition, but soon the dominant caught on and followed the subordinate in order to take the reward from her. Then the subordinate delayed her approach to the food to avoid the dominant's exploitation, and at this point, the dominant stopped following as closely. But somehow the subordinate 'gave away' information to the dominant, who continued to obtain the food reward on several trials. However, describing the chimpanzees as acting this way is anthropomorphic and anecdotal, and insufficient as a scientific report; proper analyses must be done to show the actual behavioural patterns.

After looking at the analyses of this experimental paradigm in several prior publications, I felt that so much detail was lacking; it is difficult to show how each subject's behaviour changes over time, and how it changes in relation to the other subject's changing tactics. The previous analyses could not capture the dynamic and fluid element of the interaction, which motivated the use of the cross correlations in my current study. The cross correlations allow me to examine whether one individual's behaviour is contingent on her opponent's by correlating not only when both individuals perform the referent and target action, but also when they both do not perform it, thus capturing all combinations of their actions. Furthermore, by breaking down the dataset into three phases, I can analyse one individual's behaviour that may have a particularly important impact on the competitor for only a portion of the dataset, though when analysed for the entire dataset does not appear to have any effect; this can demonstrate changes in both subjects' behaviour through time. The cross correlation method is an in-depth and detailed look into the chimpanzees' simultaneous and sequential actions, whether they are contingent between subjects, and whether they change through time; this allows me to discuss how and why the chimpanzees change their tactics in the informed forager paradigm.

C. Analysis of Walking Towards the Bait During *Competition*

Here I use cross correlations to address the subjects' movement towards the hidden bait; as shown in Figures 5.1 and 5.2, the dominant did retrieve the bait on one quarter of the trials—but how did she arrive at the hiding place? It is possible that the dominant was able to find the bait by searching randomly, by using an olfactory cue, or by using a movement cue given by the knowledgeable subordinate. I address the hypothesis that the dominant uses the subordinate's movement to guide her own by asking, "When the subordinate walks towards the bait, does the dominant walk towards the bait?" (Figure 5.4; graphs for *No Knowledge* and *Full Knowledge* controls are included in the appendix to Chapter 5, figures 5.1 and 5.2).

It appears that whether the dominant walked towards the bait is contingent on the subordinate first moving in that direction: before the subordinate walked at time= 0, the dominant was significantly unlikely to be walking towards the bait, but just three seconds after the subordinate started walking, the dominant was walking towards the bait significantly more than expected from the within-trial shuffle (Figure 5.4). When the reverse question is asked (i.e., whether the subordinate walks towards the bait after the dominant starts walking towards it), it appears that the subordinate had already been walking towards the bait by the time the dominant started towards it (Figure 5.5). Presumably the dominant did not walk towards the bait because she did not know where it was, and her movement towards the bait very shortly after the subordinate began to walk may indicate following behaviour.

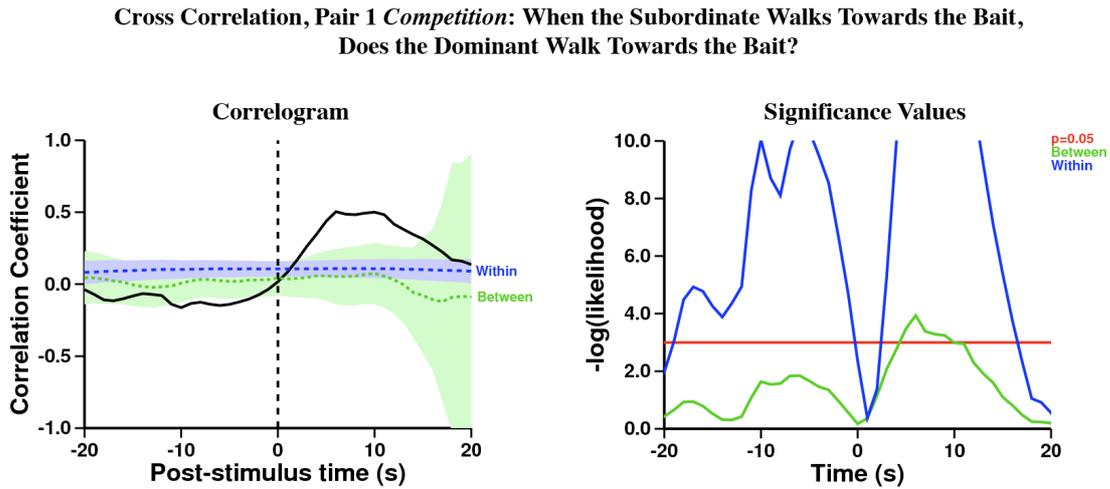


FIGURE 5.4: Referent behaviour: subordinate walking towards the bait. Target behaviour: dominant walking towards the bait. After the subordinate started to walk towards the bait, the dominant also walked towards the bait significantly more than expected from the within-trial shuffle (peak at time= +6, $r = 0.5039$, $n = 194$; $-\log\text{-likelihood} = 21.4229$, $p < 0.05$). Furthermore, before the subordinate walked (time= -19 to -1), the dominant was walking towards the bait significantly less than expected from the within-trial shuffled control (peak at time= -6, $r = -0.1481$, $n = 324$; $-\log\text{-likelihood} = 10.7046$, $p < 0.05$).

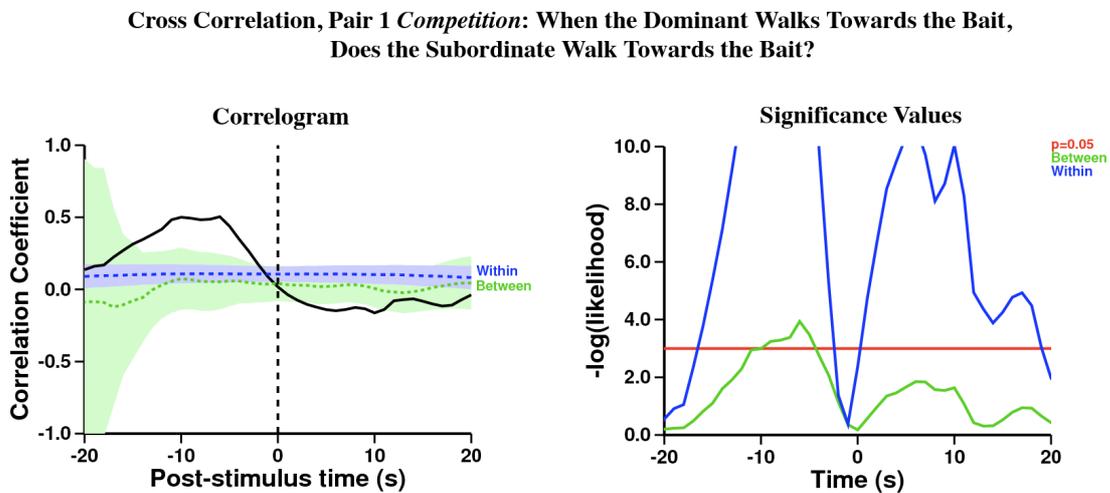


FIGURE 5.5: Referent behaviour: dominant walking towards the bait. Target behaviour: subordinate walking towards the bait. After the dominant started to walk towards the bait, the subordinate had already been walking towards it significantly more than expected from the within-trial shuffled control. This data is the same as in Figure 5.4: the cross correlation with the referent and target swapped results in a graph that is reversed in time along the x-axis.

To address whether the dominant was not acting due to the presence of the bait at a particular location, e.g., an olfactory cue, I analysed whether the chimpanzees both walked towards the same absolute quadrant of the enclosure, regardless of the location of the bait.

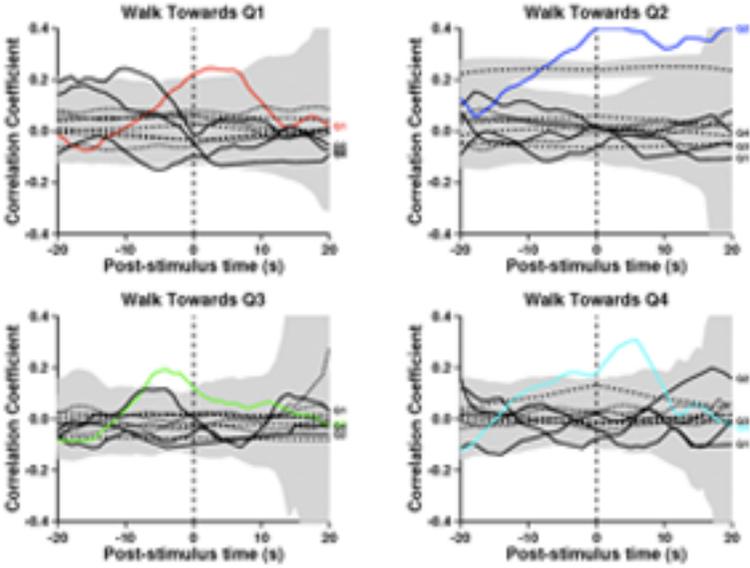
D. Analysis of Walking Towards Absolute Directions During *Competition*

To address the chimpanzees' movement towards the four quadrants in their enclosure I asked, "When the subordinate walks towards a quadrant, towards which quadrant does the dominant walk?" I compared the subordinate's movement towards one quadrant with the dominant's likelihood of walking towards any of the four quadrants (Figure 5.6). When the subordinate walked towards a particular quadrant, the dominant was significantly likely to be walking towards the *same quadrant* as the subordinate, rather than any other quadrant when compared to the between-trial shuffled control. This particular control is used because the data are coded in absolute terms (i.e., towards quadrants 1, 2, 3, 4): the chimpanzees were in a differently numbered quadrant on each trial, so shuffling between trials eliminated contingent relationships but maintained sequences of behaviour (see Chapter 4: Statistical Methods). Both chimpanzees moved towards the same absolute direction at the same time, when the location of the bait was not taken into account. However, the correlation coefficients for both chimpanzees walking towards Q2 are much higher than for other quadrants, and this may be explained by the layout of the enclosure as discussed in the following section. Furthermore, Q3 shows a different pattern: when the subordinate began to walk towards Q3, the dominant had already been walking towards Q3. This is an artefact of the experimental setup in which the dominant entered the enclosure from the 'Cognition Room' into Q3 before the subordinate entered.

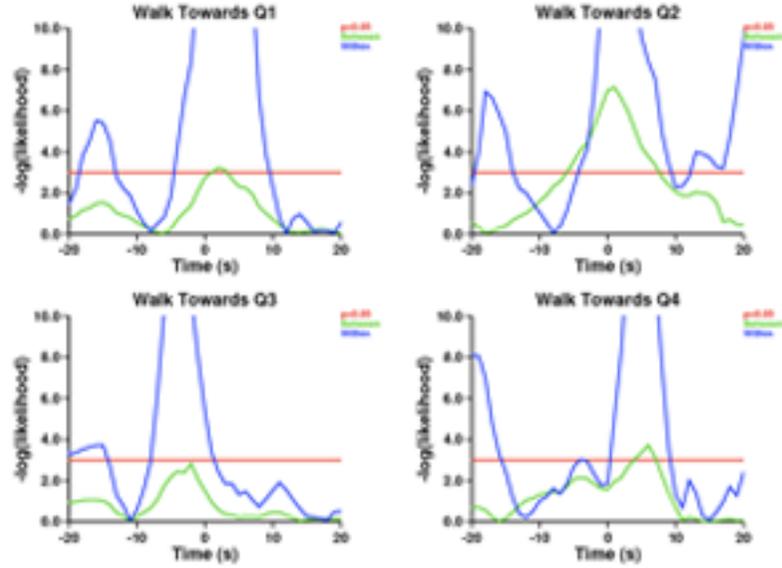
FIGURE 5.6 (next page): In each panel, the referent behaviour at time= 0 is the subordinate walking towards the quadrant of that panel (the layout corresponds to the physical layout of the enclosure). The coloured line in each panel represents the cross correlation of the dominant walking towards the same quadrant as the subordinate. The three solid black lines represent the cross correlation of the dominant walking towards each of the other three quadrants. The dotted lines with the gray spread represent the within- and between-trial shuffled controls and their standard errors of the mean. For example, in the top left panel, the referent behaviour at time= 0 is the subordinate walking towards Q1 and it is correlated with the target behaviour of the dominant walking towards Q1, and this relationship is plotted with a red line. The black lines show the cross correlations of the subordinate walking towards Q1 with the dominant walking towards Q2, Q3, and Q4. As shown below, after the subordinate started walking towards Q1 (time= +2, $r = 0.2446$, $n = 810$; $-\log\text{-likelihood} = 3.2152$, $p < 0.05$), Q2 (time= +1, $r = 0.4262$, $n = 831$; $-\log\text{-likelihood} = 7.1396$, $p < 0.05$), and Q4 (time= +6, $r = 0.3069$, $n = 719$; $-\log\text{-likelihood} = 3.7265$, $p < 0.05$), the dominant walked towards the same quadrant as the subordinate significantly more than expected from the between-trial shuffled control. The dominant walked towards Q3 before the subordinate (peak at time= -2, $r = 0.0827$, $n = 810$; $-\log\text{-likelihood} = 2.8218$, *ns*).

Cross Correlations, Pair 1 *Competition*: When the Subordinate Walks Towards a Quadrant, Towards Which Quadrant Does the Dominant Walk?

Correlograms



Significance Values



There was a very large effect of both chimpanzees walking towards Q2, as well as the opposite pattern of the dominant walking towards Q3 before the subordinate had started walking in that direction, so I analysed how much time each chimpanzee spent currently in, and walking towards, each quadrant in the enclosure to determine if these results were artefactual due to the experimental setup.

E. Time Spent in Each Quadrant During *Competition*

I considered the chimpanzees' enclosure as composed of four approximately equal quadrants. The chimpanzees were released from cages in the 'Cognition Room' at the base of Q3. Given the spatial layout of the enclosure, there are differences in the amount of time subjects spent in each quadrant: Quadrant 2 is the farthest from the start position in Q3, and it naturally takes more time to travel to Q2 than to either Q1 or Q4. Additionally, subjects seemed to spend less time overall in areas farther away from their start cages, especially Q2. Table 5.1 lists the percentage of time that each subject in this pair spent *currently* in each quadrant, and Table 5.2 lists the percentage of time each spent *moving towards* each quadrant.

A one-way chi-square goodness of fit tested the null hypothesis that each subject entered each quadrant an equal number of times; whereas Missy entered each quadrant an equal number of times (3, n= 29), $\chi^2= 1.21$, *ns*, Rita showed significant differences in her pattern of entering different areas of the enclosure (3, n= 31), $\chi^2= 10.42$, $p= 0.0153$.

TABLE 5.1: Percent of time each subject spends currently in each quadrant, Pair 1

Quadrant	Missy Current	Rita Current
Q1	29.89%	17.49%
Q2	4.95%	2.07%
Q3	55.48%	77.77%
Q4	9.68%	2.67%

TABLE 5.2: Percent of time each subject spends moving towards each quadrant, Pair 1

Quadrant	Missy Direction	Rita Direction
Q1	17.74%	18.87%
Q2	18.4%	13.74%
Q3	9.35%	9.58%
Q4	13.76%	11.36%
0 (No Locomotion)	40.75%	46.44%

Similarly, the distribution of time that the pair spent together in the same quadrant is different for each location (Table 5.3). Overall, when both subjects were outside (69.7% of all trials), they were both in the same quadrant 62.9% of the time. Of this total time spent together, they spent the majority of their time, 75.0%, in Quadrant 3. Of the total time spent together, 20.7% was in Quadrant 1. There was a side bias towards the left side of the enclosure (Quadrants 1 and 3), as they only spent time in Quadrants 2 and 4 for 0.56% and 3.73% of the time that they were together in the same quadrant, respectively.

TABLE 5.3: Percent of time spent together in each quadrant, of the overall time spent together outside, Pair 1

Quadrant	Time
Q1	20.7%
Q2	0.56%
Q3	75.0%
Q4	3.73%

Both chimpanzees spent the majority of their time on the left side of the enclosure in Quadrants 1 and 3, and the most time walking towards the back of the enclosure to Quadrants 1 and 2. They spent so little time especially in Q2, because it is so far away from their starting position in Q3; it is possible that walking towards Q2 may have elicited a strong response in the competitor to also walk towards Q2. The large effect seen when both chimpanzees walked towards Q2, and the opposite pattern of the subordinate walking towards Q3 after the dominant, must be due to the layout of the enclosure, as well as the chimpanzees' tendency to stay closer to the 'Cognition Room.'

When the chimpanzees' walking behaviour is analysed in terms of relative position in the enclosure (e.g., towards the bait) or in terms of absolute direction (e.g., towards Q2), both subjects walk towards the same location upon the subordinate's movement cue at time= 0. The exception is when they walked towards Q3: because the dominant entered the enclosure first, the pattern was reversed in Q3 and the subordinate walked on the dominant's cue. Overall, the general pattern of walking towards the same quadrant at the same time may indicate that the ignorant dominant was following the knowledgeable subordinate in order to exploit her foraging success. However, an analysis of whether both chimpanzees walk towards the same quadrant at the same time does not reveal the subtler interactions that may be taking place: the dominant may be acting in distinct ways such as *approaching* the

subordinate's current location, following in her *footsteps*, or *converging* on her destination. Furthermore, these strategies may differ over the course of the *Competition*; the dominant may change tactics as her foraging success changes, based on the subordinate's movements.

F. Approach

I will describe the patterns of *approaching* through the entire dataset by first asking whether the dominant *approached* the subordinate, then whether the subordinate *approached* the dominant. Recall that *approach* is defined as “the subjects are in different quadrants of the enclosure and one individual walks towards the other.” Then I will break down the analyses and ask these questions for each of the three distinct phases in order to illustrate any changes in either subject's actions. Then I will present graphs for the *No Knowledge*, *Full Knowledge*, and *No Bait, No Knowledge* conditions.

1. Entire Competition dataset

For the entire *Competition* dataset, when the chimpanzees were in different quadrants, the dominant *approached* the subordinate significantly more than expected compared to the within-trial shuffled control (Figure 5.7). This particular control is used because the data are collapsed (same/different quadrant, rather than quadrants 1, 2, 3, 4): because the chimpanzees being in “different” quadrants on trial one does not necessarily connote the same physical places as when they are in “different” quadrants on trial two, a within-trial shuffle is more appropriate because it maintains the behavioural contingencies between subjects but eliminates the sequences of behaviour (see Chapter 4: Statistical Methods).

**Cross Correlation, Pair 1 Competition: When Both Chimpanzees are in Different Quadrants,
Does the Dominant Walk Towards the Subordinate?**

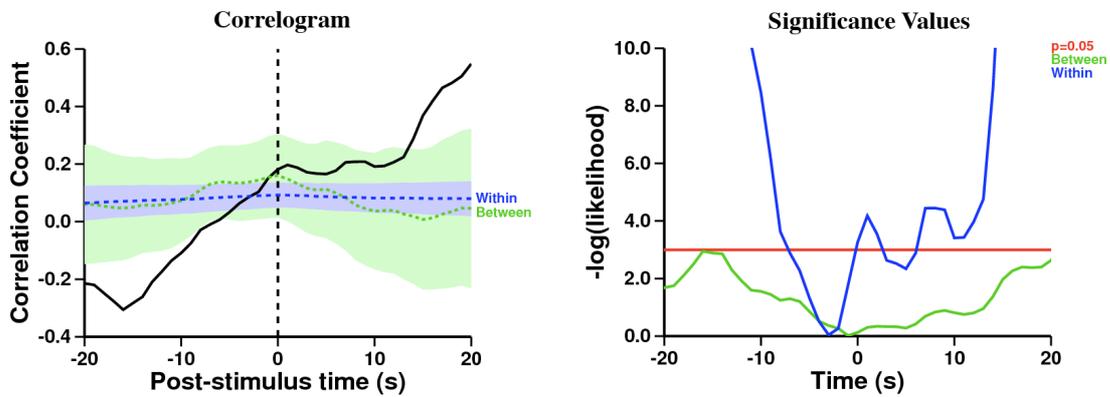


FIGURE 5.7: Referent behaviour: chimpanzees are in different quadrants. Target behaviour: dominant walking towards the subordinate. After the chimpanzees were in different quadrants, the dominant walked towards the subordinate significantly more than expected from the within-trial shuffled control (peak at time= +20, $r= 0.5483$, $n= 159$; $-\log\text{-likelihood} = 27.3684$, $p<0.05$). Furthermore, before the chimpanzees were in different quadrants (before time= 0), the dominant was walking towards the subordinate significantly less than expected from the within-trial shuffled control (peak at time= -16, $r= -0.3060$, $n= 296$; $-\log\text{-likelihood} = 23.4148$, $p<0.05$).

In order to compare the dominant's behaviour to the subordinate's, I must also ask whether the subordinate *approached* the dominant. When in different quadrants, the subordinate *approached* the dominant as well (Figure 5.8).

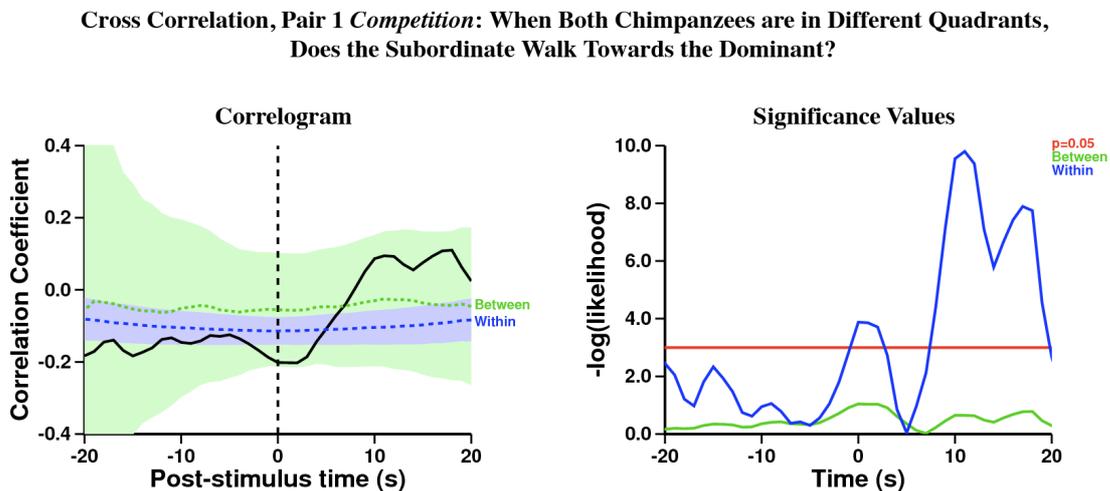


FIGURE 5.8: Referent behaviour: chimpanzees are in different quadrants. Target behaviour: subordinate walking towards the dominant. After the chimpanzees were in different quadrants, the subordinate walked towards the dominant significantly less than expected from the within-trial shuffled control between time= 0 and +2 (peak at time= 0, $r = -0.2017$, $n = 513$; $-\log\text{-likelihood} = 3.8785$, $p < 0.05$). Later, the subordinate walked towards the dominant significantly more than expected from the within-trial shuffled control (peak at time= +11, $r = 0.0944$, $n = 297$; $-\log\text{-likelihood} = 9.7993$, $p < 0.05$).

However, *approach* behaviour was not consistent throughout the 24 trials of the experiment. Therefore, I divided the analysis into three distinct phases, based on changes in the behaviour of the chimpanzees.

2. Phase 1

Approach behaviour was markedly different between the phases. During Phase 1, the dominant *approached* the subordinate, but only very briefly (Figure 5.9). During this phase the dominant usually entered the enclosure first, and climbed onto the climbing structure in the centre of the enclosure to observe the subordinate. The subordinate would then walk into the quadrant where the banana was hidden, and the dominant on the central platform would take a few steps towards the subordinate, but was limited by the surface she was standing on, and during this phase did not choose to climb down and move closer to the subordinate. After

the dominant *approached*, she stopped (Figure 5.10; “Stop” was defined as a change from “Locomotion” to five consecutive seconds of “No Locomotion”).

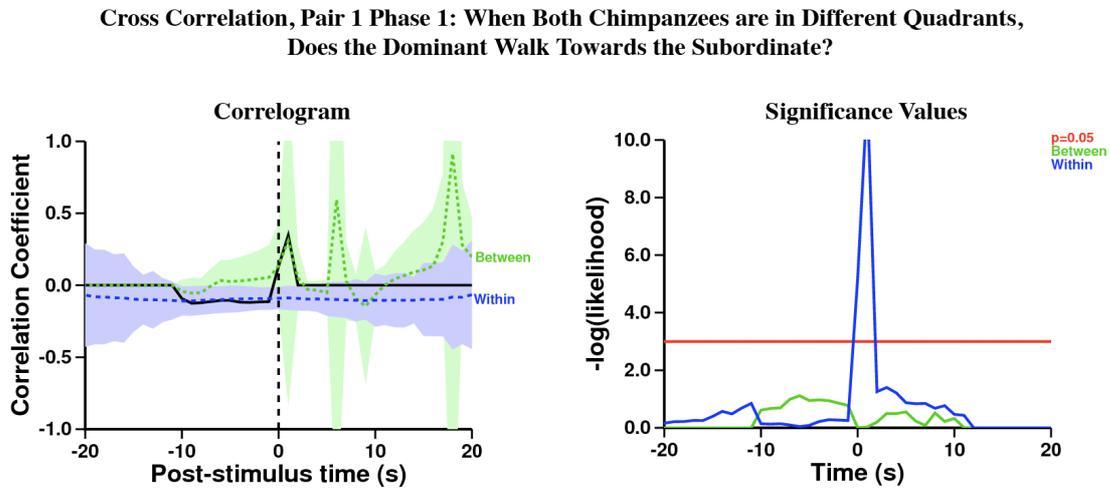


FIGURE 5.9: Referent behaviour: chimpanzees are in different quadrants. Target behaviour: dominant walking towards the subordinate. After the chimpanzees were in different quadrants, the dominant walked towards the subordinate significantly more than expected from the within-trial shuffled control (peak at time= +1, $r = 0.3468$, $n = 39$; $-\log\text{-likelihood} = 11.6007$, $p < 0.05$).

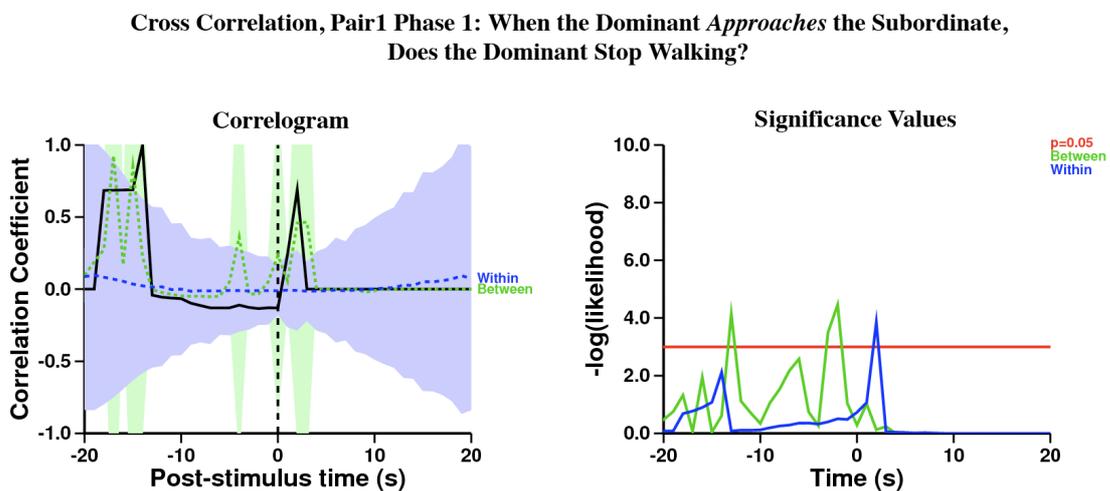


FIGURE 5.10: Referent behaviour: dominant approaching the subordinate. Target behaviour: dominant stops walking for 5 seconds. After the dominant was in a different quadrant and walked towards the subordinate, the dominant stopped walking for at least 5 seconds (peak at time= +2, $r = 0.6892$, $n = 21$; $-\log\text{-likelihood} = 3.8517$, $p < 0.05$).

In Phase 1, the subordinate walked towards the bait without interacting with the dominant, who stood on the central climbing structure observing as the subordinate retrieved the bait. There is no reason for the knowledgeable subordinate to walk towards the ignorant dominant's current location, and the results confirm that she did not approach the dominant (Figure 5.11).

Cross Correlation, Pair 1 Phase 1: When Both Chimpanzees are in Different Quadrants, Does the Subordinate Walk Towards the Dominant?

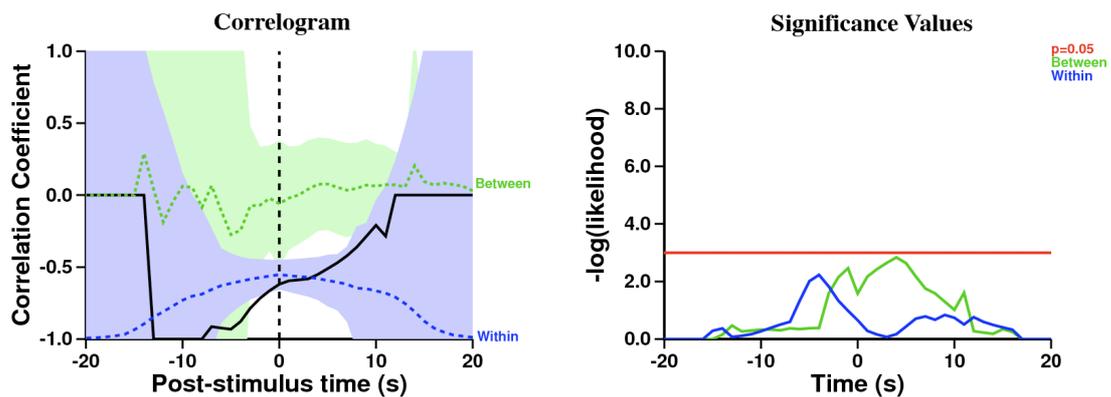


FIGURE 5.11: Referent behaviour: chimpanzees are in different quadrants. Target behaviour: subordinate walking towards the dominant. After the chimpanzees were in different quadrants, the subordinate did not walk towards the dominant: the correlation coefficient trends towards less than expected from the within-trial shuffle, (peak at time= -4, $r = -0.8778$, $n = 43$; $-\log\text{-likelihood} = 2.2289$, *ns*).

3. Phase 2

In Phase 2, the dominant again only *approached* the subordinate briefly. Before the chimpanzees were in different quadrants, the dominant walked towards the subordinate significantly more than expected from the within-trial shuffle, and then after they were in different quadrants, the dominant did not continue to walk towards the subordinate (Figure 5.12).

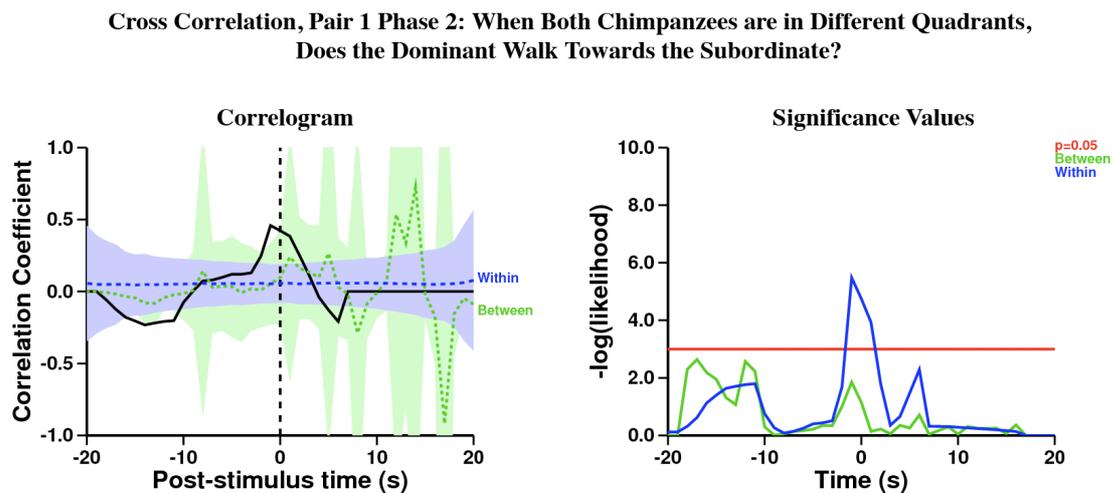


FIGURE 5.12: Referent behaviour: chimpanzees are in different quadrants. Target behaviour: dominant walking towards the subordinate. Before the chimpanzees were in different quadrants, the dominant walked towards the subordinate significantly more than expected from the within-trial shuffled control for only a few seconds (peak at time = -1, $r = 0.4585$, $n = 59$; $-\log\text{-likelihood} = 5.4801$, $p < 0.05$). After they were in different quadrants, the dominant stopped walking towards the subordinate, as the correlation coefficient trends towards being less than the within-trial shuffled control (peak at time = +6, $r = -0.2081$, $n = 34$; $-\log\text{-likelihood} = 2.2867$, ns).

Furthermore, when the dominant did *approach* the subordinate, the dominant stopped walking shortly after (Figure 5.13). It seems that the dominant would walk towards the subordinate only until the subordinate entered a different quadrant, at which point the dominant paused to observe, as she had done in Phase 1.

Cross Correlation, Pair 1 Phase 2: When the Dominant *Approaches* the Subordinate, Does the Dominant Stop Walking?

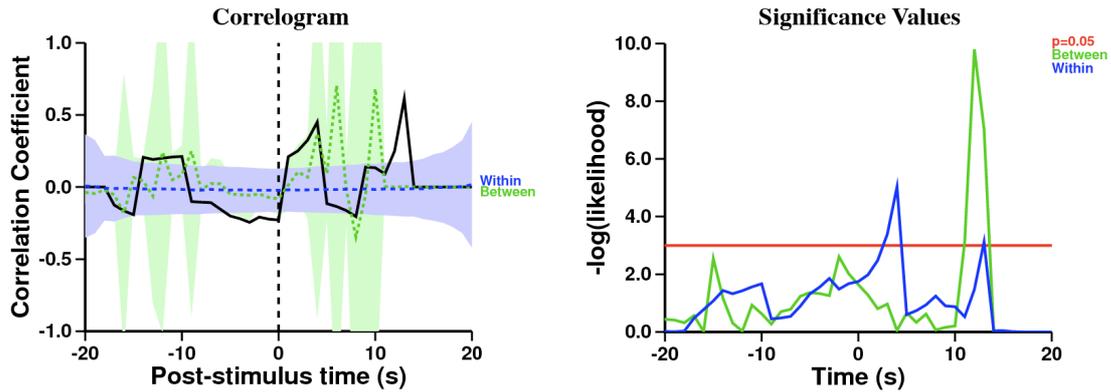


FIGURE 5.13: Referent behaviour: dominant *approaching* the subordinate. Target behaviour: the dominant stops walking for 5 seconds. Very shortly after the dominant *approached* the subordinate, she stopped walking significantly more than expected from the within-trial control (peak at time= +4, $r = 0.4507$, $n = 34$; $-\log\text{-likelihood} = 5.0299$, $p < 0.05$).

Similarly, in Phase 2, the subordinate did not *approach* the dominant; this is an expected result. When both chimpanzees were in the same quadrant, the subordinate walked towards the dominant, but not when they were in different quadrants (Figure 5.14). Both relationships are significant compared to the within-trial shuffle.

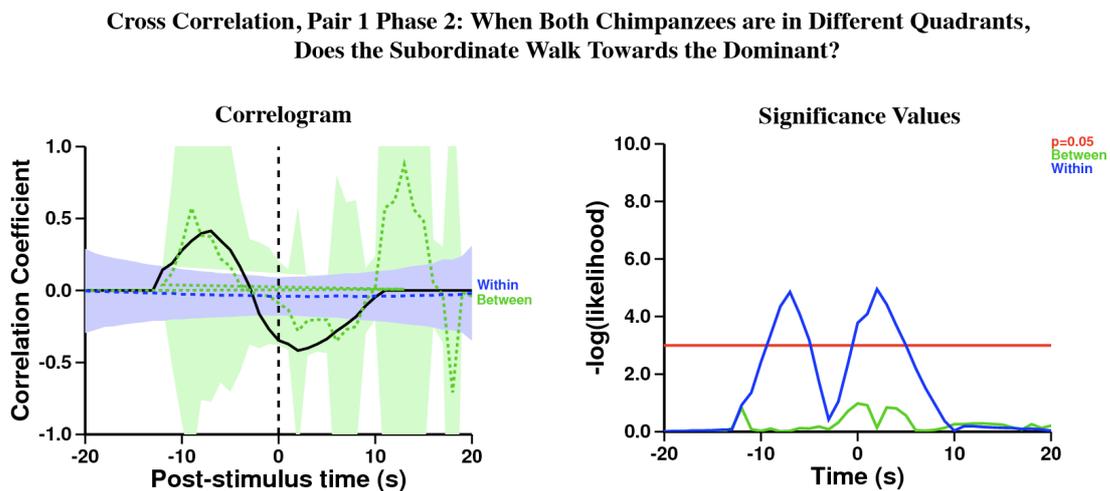


FIGURE 5.14: Referent behaviour: chimpanzees are in different quadrants. Target behaviour: subordinate walking towards the dominant. After the chimpanzees were in different quadrants, the subordinate walked towards the dominant significantly less than expected from the within-trial shuffled control (peak at time= +2, $r = 0.4176$, $n = 71$; $-\log\text{-likelihood} = 4.9505$, $p < 0.05$). Furthermore, before the chimpanzees were in different quadrants, the subordinate walked towards the dominant significantly more than expected from the within-trial shuffled control (peak at time= -7, $r = 0.4138$, $n = 41$; $-\log\text{-likelihood} = 4.8520$, $p < 0.05$).

4. Phase 3

During Phase 3 both subjects resumed *approaching*: when they were both in different quadrants, each subject walked towards her competitor (Figures 5.15 and 5.17). The subordinate avoided walking directly towards the bait on many trials in Phase 3, or walked in the wrong direction, so the best strategy for the dominant to exploit the subordinate was to *approach*, rather than to walk in her *footsteps* or *converge* on her destination.

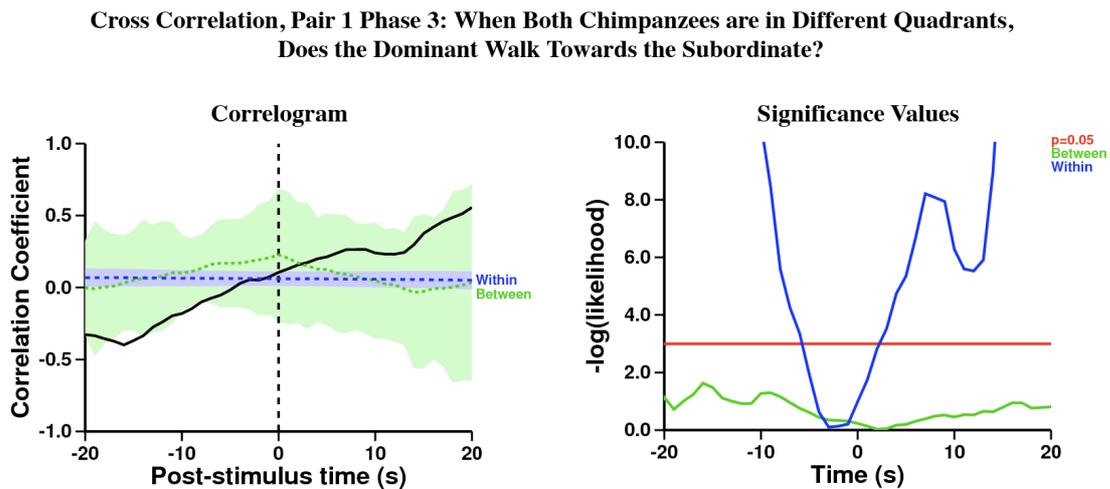


FIGURE 5.15: Referent behaviour: chimpanzees are in different quadrants. Target behaviour: dominant walking towards the subordinate. After the chimpanzees were in different quadrants, the dominant walked towards the subordinate significantly more than expected from the within-trial shuffled control (peak at time= +20, $r = 0.5565$, $n = 158$; $-\log\text{-likelihood} = 27.0787$, $p < 0.05$). Furthermore, before the chimpanzees were in different quadrants (before time= 0), the dominant walking towards the subordinate significantly less than expected from the within-trial shuffled control (peak at time= -16, $r = -0.3990$, $n = 239$; $-\log\text{-likelihood} = 27.7709$, $p < 0.05$).

The subordinate paused as the dominant approached her (Figure 5.16), most likely due to her hesitation to encounter the dominant, or perhaps in an effort to not move closer to the food reward if the dominant was physically close to it. This is similar to a previous report of informed subjects stopping when monitored by their dominant competitor (Ducoing & Thierry, 2003).

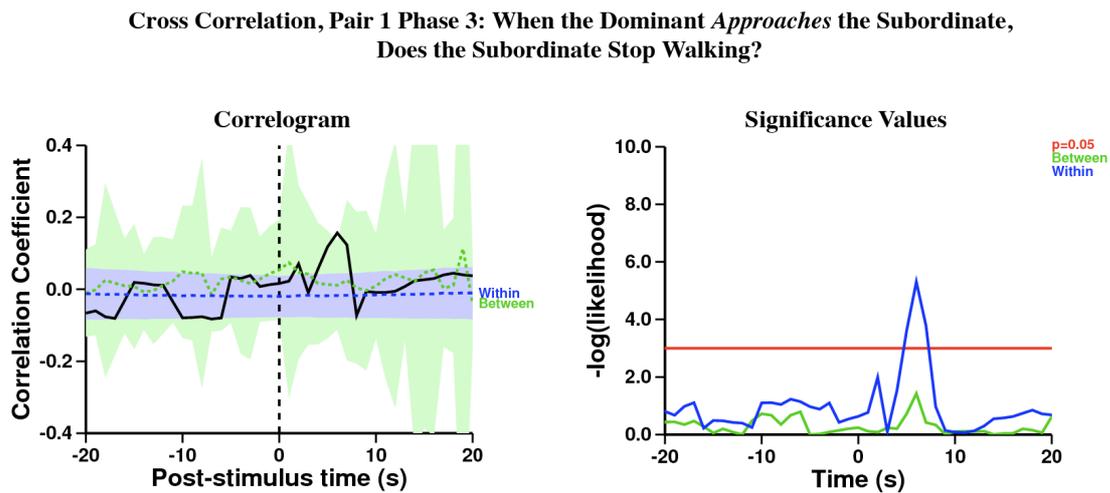


FIGURE 5.16: Referent behaviour: dominant *approaching* the subordinate. Target behaviour: subordinate stops walking for 5 seconds. After the dominant was in a different quadrant and walked towards the subordinate, the subordinate stopped walking significantly more than expected from the within-trial shuffled control (peak at time= +6, $r = 0.1567$, $n = 248$; $-\log\text{-likelihood} = 5.3072$, $p < 0.05$).

In Phase 3, the subordinate also *approached* the dominant, many seconds after they were both in different quadrants (Figure 5.17).

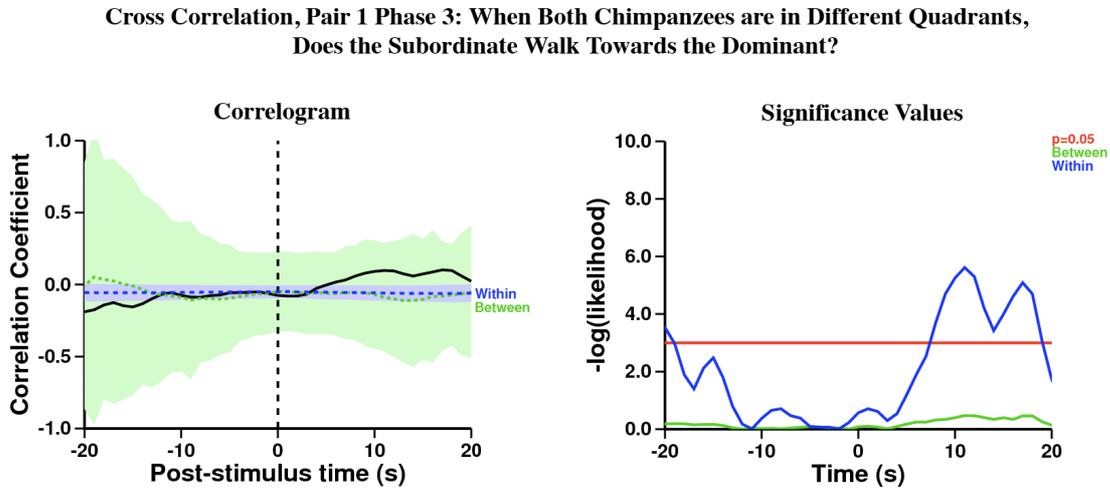


FIGURE 5.17: Referent behaviour: chimpanzees are in different quadrants. Target behaviour: subordinate walking towards the dominant. After the chimpanzees were in different quadrants, the subordinate walked towards the dominant significantly more than expected from the within-trial shuffled control, (peak at time = +11, $r = 0.0976$, $n = 248$; $-\log$ -likelihood = 5.6165, $p < 0.05$).

The overall dataset showed that both subjects *approached* their opponent, but the phase-by-phase analysis has been valuable in that it has shown that this pattern is inconsistent throughout each phase of the experiment. Before the dominant was eager to search the enclosure for the banana, she only very briefly *approached* the subordinate, and often her movement was limited because she was standing on the central climbing structure. By Phase 3 the dominant spent a lot of time *approaching* the subordinate significantly more than expected, following her all the way to the hiding place and successfully exploiting the subordinate. The subordinate counter-acted this tactic by stopping for five seconds when the dominant *approached* her. The subordinate did not *approach* the dominant at all until the third phase of the experiment, and only after spending several seconds in a different quadrant did the subordinate walk towards the dominant.

5. No Knowledge controls

During the control trials, the *approach* behaviour was very different between the two subjects. In the *No Knowledge* controls, the dominant did *approach* the subordinate, albeit less than during the *Competition* (Figure 5.18). The dominant had learned over the course of

20 competitive trials that *approaching* the subordinate was an effective tactic to gain information from her about the food's location, and so this tactic was not abandoned during the *No Knowledge* controls, especially since the subordinate found a banana by on the first control trial.

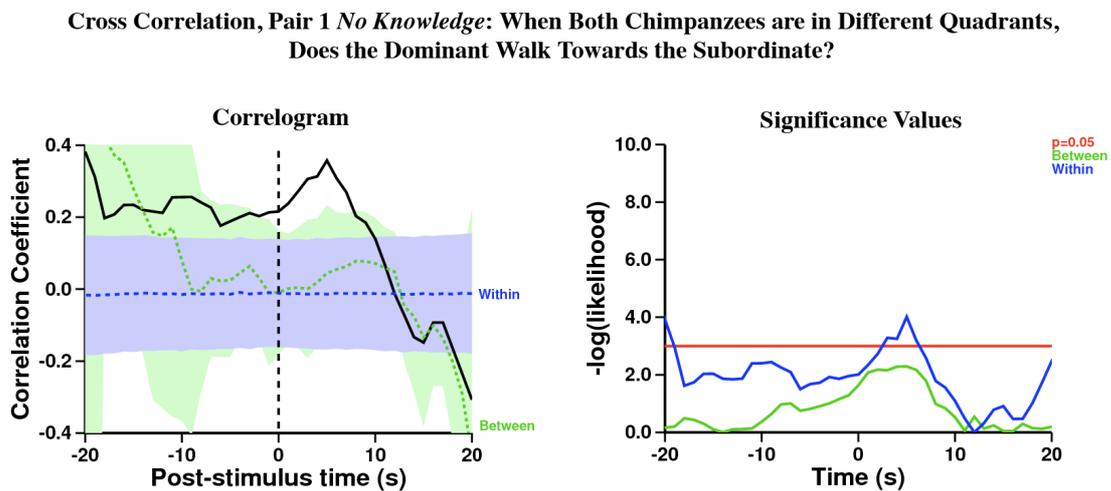


FIGURE 5.18: Referent behaviour: chimpanzees are in different quadrants. Target behaviour: dominant walking towards the subordinate. After the chimpanzees were in different quadrants, the dominant walked towards the subordinate significantly more than expected from the within-trial shuffled control between time= +3 to +6 (peak at time= +5, $r=0.3575$, $n=77$; $-\log\text{-likelihood}=4.4014$, $p<0.05$).

In the *No Knowledge* controls, the subordinate *approached* the dominant many seconds after they were in different quadrants (Figure 5.19).

Cross Correlation, Pair 1 *No Knowledge*: When Both Chimpanzees are in Different Quadrants, Does the Subordinate Walk Towards the Dominant?

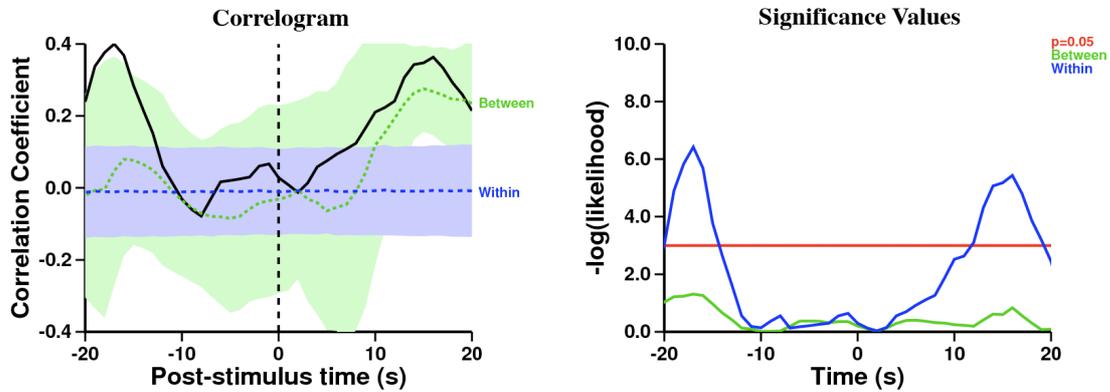


FIGURE 5.19: Referent behaviour: chimpanzees are in different quadrants. Target behaviour: subordinate walking towards the dominant. After the chimpanzees were in different quadrants, the subordinate walked towards the dominant significantly more than expected between time= +12 and +19 (peak at time= +16, $r = 0.3633$, $n = 69$; $-\log\text{-likelihood} = 5.4338$, $p < 0.05$). Also, many seconds before the chimpanzees were in different quadrants, the subordinate walked towards the dominant for a brief period between time= -20 to -15. (peak at time= -17, $r = 0.4000$, $n = 90$; $-\log\text{-likelihood} = 6.4201$, $p < 0.05$).

6. Full Knowledge controls

On the other hand, during the *Full Knowledge* control trials, there were no data (and therefore no figure) showing that the dominant approached the subordinate: when the dominant had seen where the food was hidden she immediately ran towards it and did not rely on any cue from the subordinate in order to inform her search, and therefore did not walk towards her. On the other hand, the subordinate did not walk towards the dominant when they were in different quadrants in this control condition, but did walk towards her in the few seconds that they were in the same quadrant, although this relationship was not significant (Figure 5.20).

Cross Correlation, Pair 1 *Full Knowledge*: When Both Chimpanzees are in Different Quadrants, Does the Subordinate Walk Towards the Dominant?

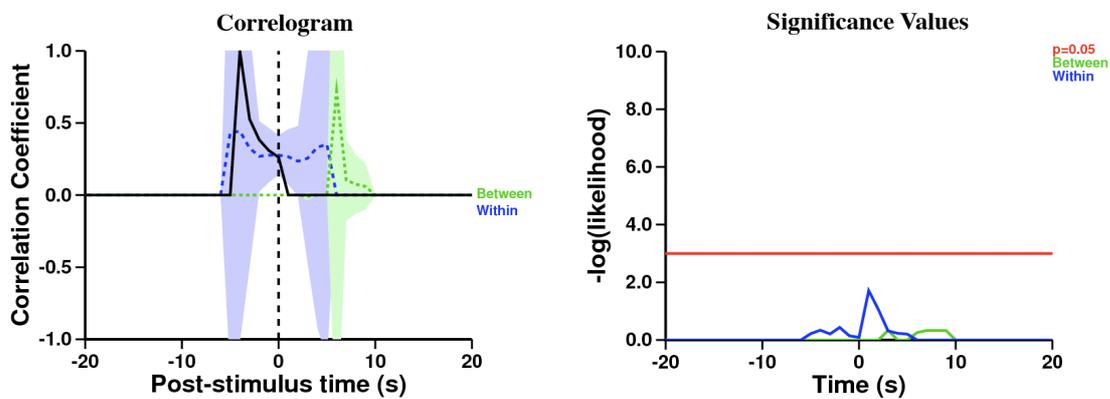


FIGURE 5.20: Referent behaviour: chimpanzees are in different quadrants. Target behaviour: subordinate walking towards the dominant. The subordinate walked towards the dominant before they were in different quadrants, and this relationship only trended towards being different from the within-trial shuffled control (time= +1, $r = 0.0000$, $n = 21$; $-\log$ -likelihood = 1.7109, *ns*).

7. No Bait, No Knowledge controls

During the *No Bait, No Knowledge* controls, neither subject *approached* the other, and in fact the subordinate was significantly unlikely to *approach* the dominant (Figures 5.21 and 5.22).

Cross Correlation, Pair 1 *No Bait, No Knowledge*: When Both Chimpanzees are in Different Quadrants, Does the Dominant Walk Towards the Subordinate?

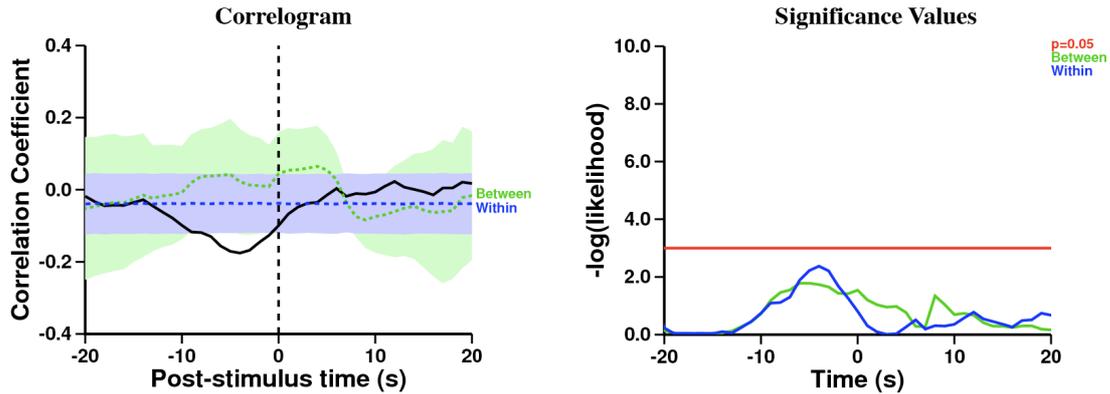


FIGURE 5.21: Referent behaviour: chimpanzees are in different quadrants. Target behaviour: dominant walking towards the subordinate. The dominant did not walk towards the subordinate before they were in different quadrants, and this relationship only trends towards being different from the within-trial shuffled control (peak at time = -4, $r = -0.1757$, $n = 204$; $-\log\text{-likelihood} = 2.3722$, *ns*). The dominant did not *approach* the subordinate when they were in different quadrants.

Cross Correlation, Pair 1 *No Bait, No Knowledge*: When Both Chimpanzees are in Different Quadrants, Does the Subordinate Walk Towards the Dominant?

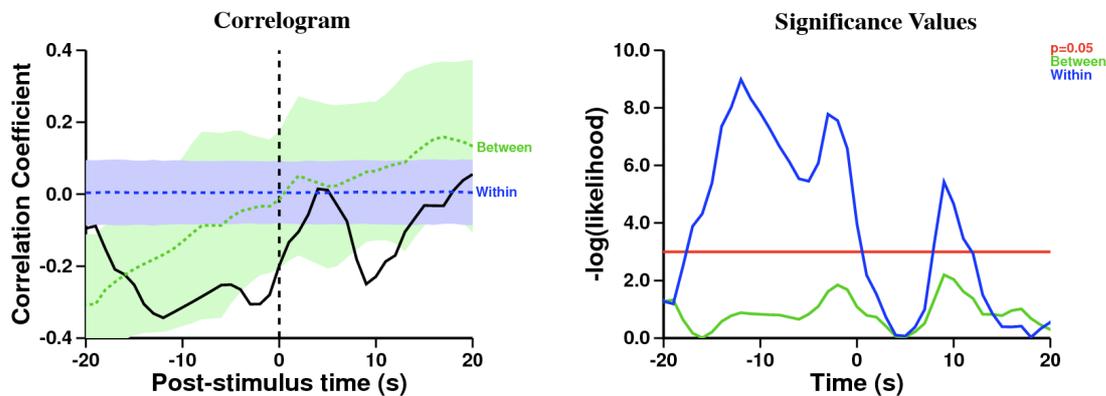


FIGURE 5.22: Referent behaviour: chimpanzees are in different quadrants. Target behaviour: subordinate walking towards the dominant. The subordinate walked towards the dominant significantly less than expected before they were in different quadrants, between time= -17 and 0 (peak at time= -12, $r = -0.3436$, $n = 159$; $-\log\text{-likelihood} = 8.9833$, $p < 0.05$). After the chimpanzees were in different quadrants, the subordinate walked towards the dominant significantly less than the within-trial shuffled control between time= +8 and +11 (peak at time= +9, $r = -0.2498$, $n = 135$; $-\log\text{-likelihood} = 5.4278$, $p < 0.05$).

8. Summary of *Approach* Behaviour

Approach behaviour was found to be different both between subjects and between different phases of the *Competition*, which may reflect the different movement types used by each chimpanzee. Overall, both chimpanzees *approached* the other. During Phase 1, the dominant *approached* the subordinate very briefly, but the subordinate walked straight to the bait without *approaching* the dominant. In Phase 2, neither chimpanzee *approached* the other. In Phase 3, both chimpanzees *approached* her opponent. In the *No Knowledge* controls, the dominant continued to *approach* the subordinate, and the subordinate *approached* the dominant after some time. In the *Full Knowledge* controls, the dominant walked straight to the bait without *approaching* the subordinate, and the subordinate only walked towards the dominant when they were together in the same quadrant. In the *No Bait, No Knowledge* controls, neither subject *approached* the other.

G. *Footsteps*

Similar to *approach* behaviour, I will describe the patterns of walking in the other's *footsteps* in the same manner for the entire dataset, for each of the three distinct phases, and then for the three controls. *Footsteps* was defined as “both subjects are in the same quadrant

and both are walking towards the same (any) quadrant, and one individual is walking towards the other and the other walking away from the first individual.”

1. Entire *Competition* dataset

While there was a strong pattern of each chimpanzee walking towards the other when they were in different quadrants (*approach*), I must also address whether the chimpanzees walked towards each other while in the same quadrant. It could be the case that when the two chimpanzees are in close proximity the dominant can better intimidate or exploit the subordinate than when they are far apart; hence, when they are in the same quadrant together, the dominant may search on her own without closely following in the *footsteps* of the subordinate, but when they are in different quadrants the dominant may make a greater effort to close the distance between her competitor. To address this question, I asked, “When both chimpanzees are in the same quadrant and walking towards the same quadrant, does the dominant walk towards the subordinate, and the subordinate walk away from the dominant?” The cross correlation shows that there is only a trend towards significance for either chimpanzee walking in the *footsteps* of the other (Figures 5.23 and 5.24).

Cross Correlation, Pair 1 *Competition*: When Both Chimpanzees are in the Same Quadrant and Walking Towards the Same Quadrant, Does the Dominant Walk Towards the Subordinate, and the Subordinate Walk Away From the Dominant?

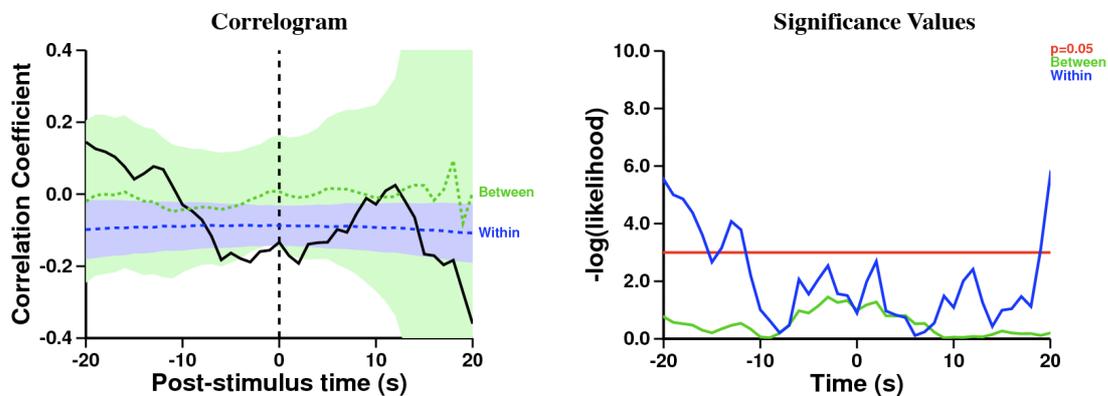


FIGURE 5.23: Referent behaviour: chimpanzees are both in the same quadrant and both walking towards the same quadrant. Target behaviour: dominant walking towards the subordinate and the subordinate walking away from the dominant. After the chimpanzees were in the same quadrant and walking towards the same quadrant, the dominant did not walk towards the subordinate and the subordinate walk away from the dominant; this relationship trends towards being less than expected from the within-trial shuffled control for a few seconds before and after time= 0 (peak at time= +2, $r = -0.1924$, $n = 244$; $-\log\text{-likelihood} = 2.6905$, *ns*), then trends towards being more than expected from the within-trial shuffled control (peak at time= +12, $r = 0.0249$, $n = 101$; $-\log\text{-likelihood} = 2.4140$, *ns*). At either far end of the correlogram, the data becomes significantly different from the within-trial shuffled control, indicating that many seconds before the chimpanzees were in the same quadrant and walking towards the same quadrant, the dominant was walking towards the subordinate and the subordinate away from the dominant (peak at time= -20, $r = 0.1449$, $n = 94$; $-\log\text{-likelihood} = 5.5432$, $p < 0.05$); and many seconds after the chimpanzees were in the same quadrant and walking towards the same quadrant, the dominant did not walk towards the subordinate and the subordinate did not walk away from the dominant (peak at time= +20, $r = -0.3600$, $n = 66$; $-\log\text{-likelihood} = 5.7009$, $p < 0.05$).

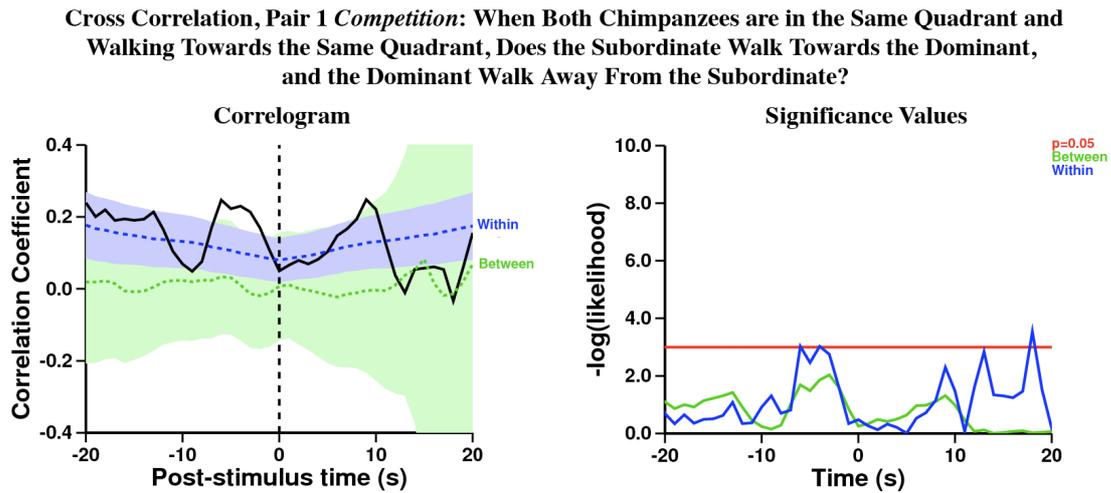


FIGURE 5.24: Referent behaviour: chimpanzees are both in the same quadrant and both walking towards the same quadrant. Target behaviour: subordinate walking towards the dominant and the dominant walking away from the subordinate. After the chimpanzees were in the same quadrant and walking towards the same quadrant, the subordinate walked towards the dominant and the dominant walked away from the subordinate; this relationship trends towards being more than expected from the within-trial shuffled control (peak at time= +9, $r = 0.2483$, $n = 134$; $-\log\text{-likelihood} = 2.2954$, ns), then becomes significantly less than expected from the within-trial shuffled control (time= +18, $-r = 0.0337$, $n = 76$; $-\log\text{-likelihood} = 3.5399$, $p < 0.05$). Furthermore, before the chimpanzees were both in the same quadrant and both walking towards the same quadrant, the subordinate walked towards the dominant and the dominant walked away from the subordinate significantly more than expected from the within-trial shuffled control (peak at time= -4, $r = 0.2299$, $n = 237$; $-\log\text{-likelihood} = 3.0262$, $p < 0.05$).

2. Phase 1

Again, this behaviour is different between the three phases. This behaviour is less common than *approaching* and is not significant, overall or in any one phase. Despite this, it is useful to observe the pattern in the data: whether the correlation coefficients increase or decrease. During Phase 1 there are no data showing the dominant walking in the subordinate's *footsteps* (and therefore no figure), however the pattern in the data clearly shows that the subordinate did not walk in the dominant's *footsteps* (Figure 5.25). During this phase, the subordinate walked directly to the bait and did not pay much attention to the dominant's movements, and the dominant made no attempt to exploit the subordinate by

following her.

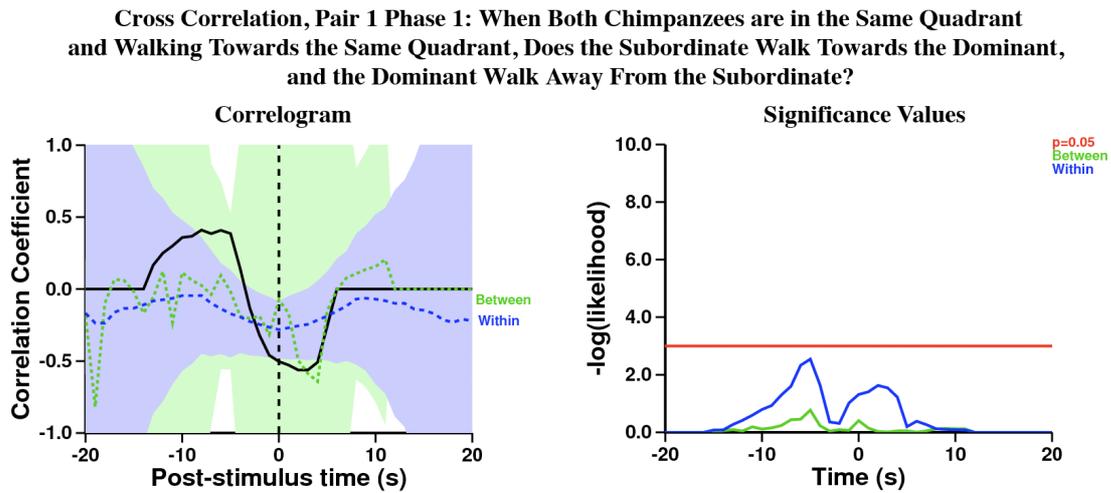


FIGURE 5.25: Referent behaviour: chimpanzees are both in the same quadrant and both walking towards the same quadrant. Target behaviour: subordinate walking towards the dominant and the dominant walking away from the subordinate. After the chimpanzees were in the same quadrant and walking towards the same quadrant, the subordinate did not walk towards the dominant and the dominant walk away from the subordinate; this relationship trends towards being less than expected from the within-trial shuffled control for a few seconds before and after time= 0 (peak at time= +2, $r = -0.5628$, $n = 33$; $-\log\text{-likelihood} = 1.6276$, *ns*). Furthermore, before the chimpanzees were in the same quadrant and walking towards the same quadrant, the subordinate walked towards the dominant and the dominant walked away from the subordinate; this relationship trends towards being more than expected from the within-trial shuffled control (peak at time= -5, $r = 0.3855$, $n = 25$; $-\log\text{-likelihood} = 2.5423$, *ns*).

3. Phase 2

However, in Phase 2 the dominant had learned over successive trials that the subordinate had found a valuable food reward, and the dominant began to follow her closely. Though it was not significant, the pattern in the correlogram clearly shows that the dominant followed in the *footsteps* of the subordinate (Figure 5.26).

Cross Correlation, Pair 1 Phase 2: When Both Chimpanzees are in the Same Quadrant and Walking Towards the Same Quadrant, Does the Dominant Walk Towards the Subordinate, and the Subordinate Walk Away From the Dominant?

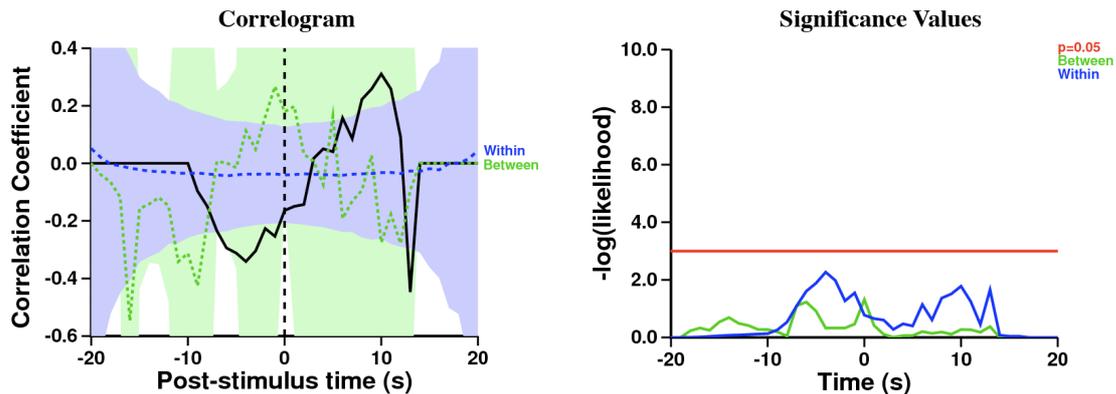


FIGURE 5.26: Referent behaviour: chimpanzees are both in the same quadrant and both walking towards the same quadrant. Target behaviour: dominant walking towards the subordinate and the subordinate walking away from the dominant. After the chimpanzees were in the same quadrant and walking towards the same quadrant, the dominant walked towards the subordinate and the subordinate walked away from the dominant; this relationship trends towards being more than expected from the within-trial shuffled control (peak at time= +10, $r = 0.3105$, $n = 11$; $-\log\text{-likelihood} = 1.7777$, *ns*). Furthermore, before the chimpanzees were in the same quadrant and walking towards the same quadrant, the dominant did not walk towards the subordinate and the subordinate did not walk away from the dominant; this relationship trends towards being less than expected from the within-trial shuffled control (peak at time= -4, $r = -0.3411$, $n = 41$; $-\log\text{-likelihood} = 2.2669$, *ns*).

In Phase 2 the subordinate maintained her behaviour, she did not follow in the *footsteps* of the dominant (Figure 5.27).

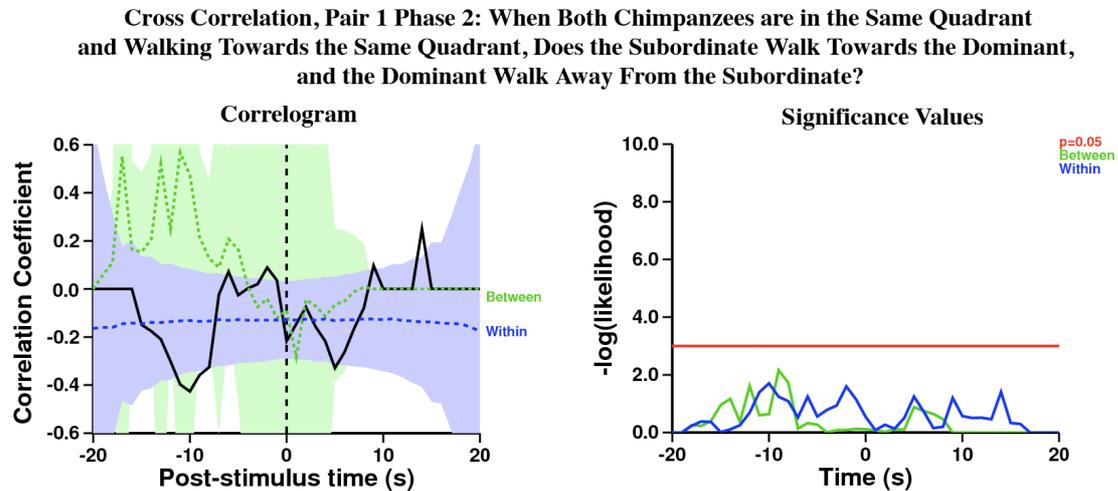


FIGURE 5.27: Referent behaviour: chimpanzees are both in the same quadrant and both walking towards the same quadrant. Target behaviour: subordinate walking towards the dominant and the dominant walking away from the subordinate. After the chimpanzees were in the same quadrant and walking towards the same quadrant, there is no significant relationship of the subordinate walking towards the dominant and the dominant walking away from the subordinate, though the pattern of the data shows that the subordinate is not following in the dominant's footsteps.

4. Phase 3

In Phase 3, several seconds after both chimpanzees were in the same quadrant and walking in the same direction together, the dominant's *footsteps* behaviour trended towards significance (Figure 5.28).

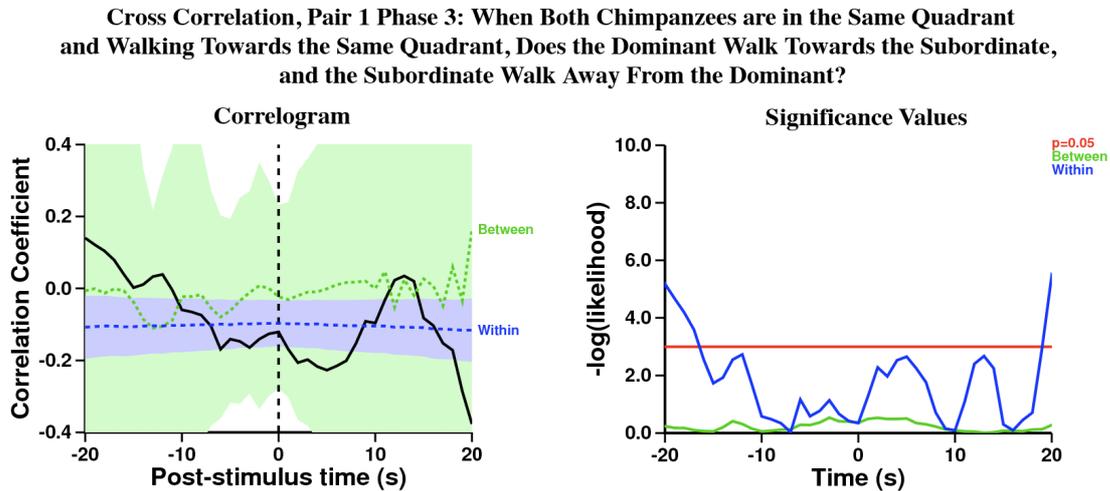


FIGURE 5.28: Referent behaviour: chimpanzees are both in the same quadrant and both walking towards the same quadrant. Target behaviour: dominant walking towards the subordinate and the subordinate walking away from the dominant. After the chimpanzees were in the same quadrant and walking towards the same quadrant, the dominant did not walk towards the subordinate and the subordinate did not walk away from the dominant; this relationship trends towards being less than expected from the within-trial shuffled control for a few seconds after time= 0 (peak at time= +5, $r = -0.2272$, $n = 142$; $-\log\text{-likelihood} = 2.6529$, ns). Eight seconds later, the relationship trends towards being more than expected from the within-trial shuffled control (peak at time= +13, $r = 0.0347$, $n = 87$; $-\log\text{-likelihood} = 2.6741$, ns).

In contrast to the dominant, the subordinate's *footsteps* behaviour became significantly less than expected from the within-trial shuffled control: the subordinate did not follow the dominant (Figure 5.29).

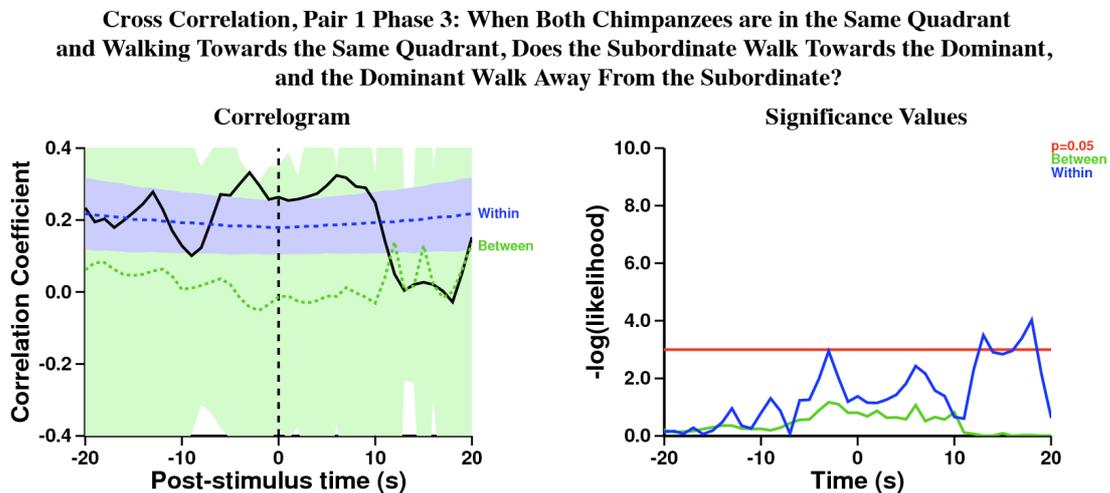


FIGURE 5.29: Referent behaviour: chimpanzees are both in the same quadrant and both walking towards the same quadrant. Target behaviour: subordinate walking towards the dominant and the dominant walking away from the subordinate. After the chimpanzees were in the same quadrant and walking towards the same quadrant, the subordinate walked towards the dominant and the dominant walked away from the subordinate; this relationship trends towards being more than expected from the within-trial shuffled control for a few seconds before and after time= 0 (peak at time= +5, $r = 0.2962$, $n = 142$; $-\log\text{-likelihood} = 2.6529$, *ns*). Thirteen seconds after time= 0, the relationship becomes significantly less than expected from the within-trial shuffled control (peak at time= +18, $r = -0.0279$, $n = 74$; $-\log\text{-likelihood} = 4.0273$, $p < 0.05$).

By splitting the dataset into three phases based on changes in the subjects' behaviour, the correlograms more accurately present *footsteps* behaviour: when the dominant was still naïve to the experimental condition in Phase 1, she did not follow in the dominant's *footsteps*, though as soon as she witnessed the subordinate pick up the banana from the hanging tire on trial 7 and became motivated to search, she followed in the subordinate's *footsteps* throughout Phase 2. By Phase 3, the subordinate stopped walking when the dominant followed in her *footsteps*, so the pattern of the dominant's movement also changed, and she used this movement type less.

5. *No Knowledge* controls

The exact opposite pattern is seen in the *No Knowledge* controls: the dominant did not follow in the *footsteps* of the subordinate (Figure 5.30), but the pattern in the correlogram of the subordinate indicates that she appeared to follow the dominant, though the relationship is not significant (Figure 5.31).

Cross Correlation, Pair 1 *No Knowledge*: When Both Chimpanzees are in the Same Quadrant and Walking Towards the Same Quadrant, Does the Dominant Walk Towards the Subordinate, and the Subordinate Walk Away From the Dominant?

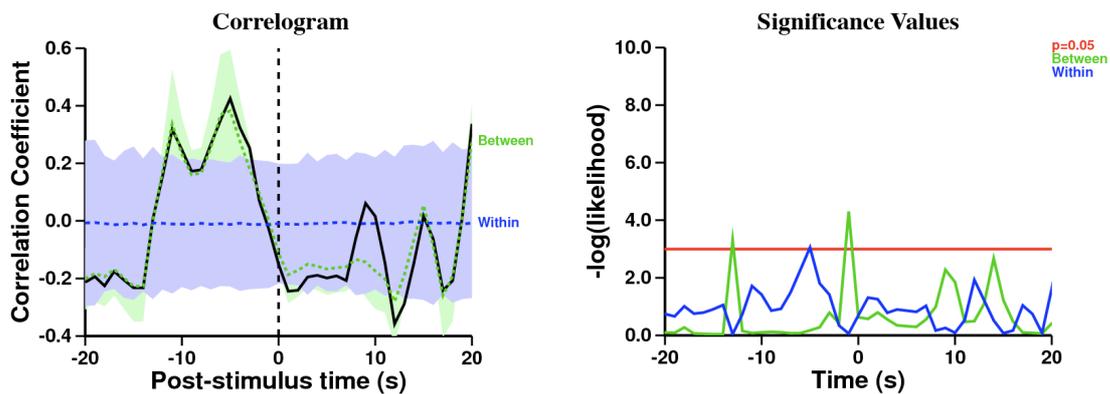


FIGURE 5.30: Referent behaviour: chimpanzees are both in the same quadrant and both walking towards the same quadrant. Target behaviour: dominant walking towards the subordinate and the subordinate walking away from the dominant. After the chimpanzees were in the same quadrant and walking towards the same quadrant, dominant did not walk towards the subordinate and the subordinate did not walk away from the dominant, though this relationship is not significant. Furthermore, before the chimpanzees were in the same quadrant and walking towards the same quadrant, the dominant walked towards the subordinate and the subordinate walked away from the dominant significantly more than expected from the within-trial shuffled control (peak at time = -5, $r = 0.4251$, $n = 53$; $-\log\text{-likelihood} = 3.0528$, $p < 0.05$).

Cross Correlation, Pair 1 *No Knowledge*: When Both Chimpanzees are in the Same Quadrant and Walking Towards the Same Quadrant, Does the Subordinate Walk Towards the Dominant, and the Dominant Walk Away From the Subordinate?

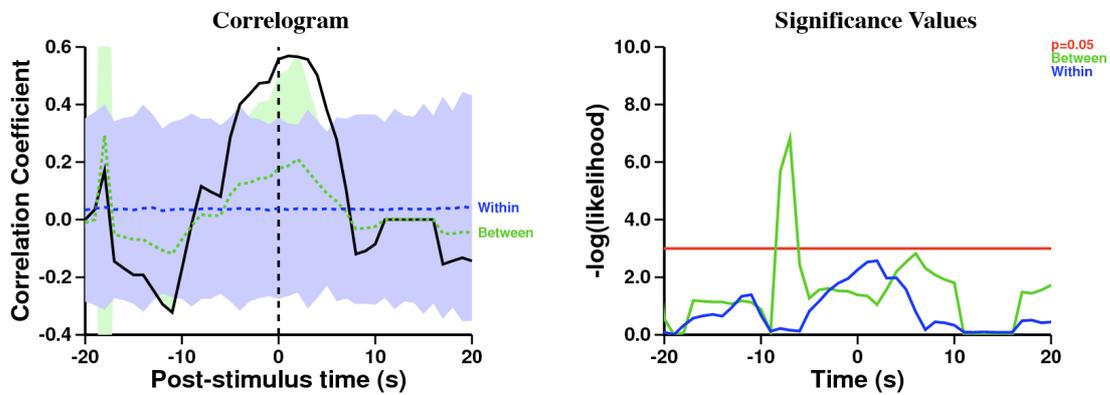


FIGURE 5.31: Referent behaviour: chimpanzees are both in the same quadrant and both walking towards the same quadrant. Target behaviour: subordinate walking towards the dominant and the dominant walking away from the subordinate. After the chimpanzees were in the same quadrant and walking towards the same quadrant, the subordinate walked towards the dominant and the dominant walked away from the subordinate; this relationship trends towards being more than expected from the within-trial shuffled control (peak at time=+2, $r = 0.5657$, $n = 54$; $-\log\text{-likelihood} = 2.5719$, ns).

6. Full Knowledge controls

Furthermore, in the *Full Knowledge* controls, because the dominant ran out so quickly into the enclosure in search of food there are no data showing *footsteps* behaviour (and therefore no figure). On the other hand, the subordinate did follow the dominant for the brief period that they were together in the same quadrant (Figure 5.32).

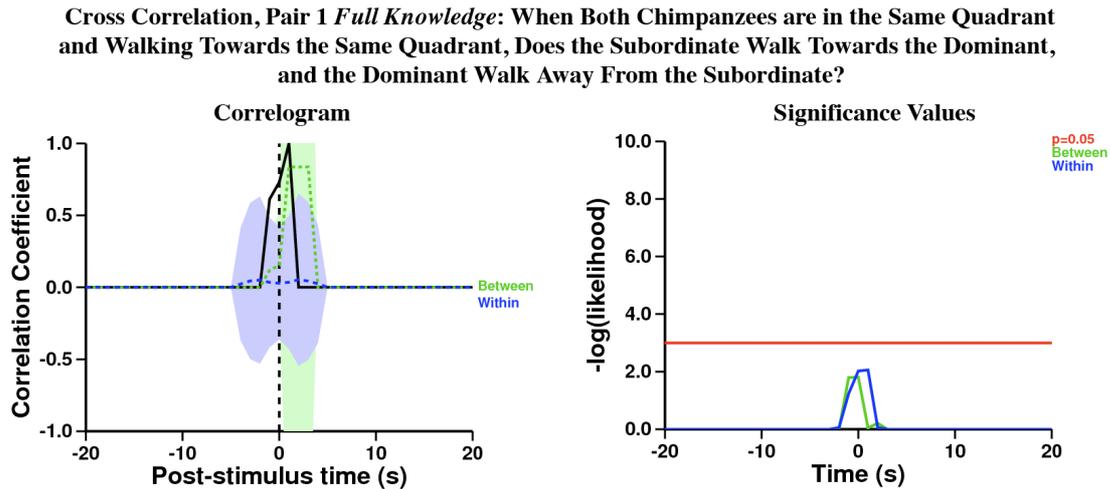


FIGURE 5.32: Referent behaviour: chimpanzees are both in the same quadrant and both walking towards the same quadrant. Target behaviour: subordinate walking towards the dominant and the dominant walking away from the subordinate. After the chimpanzees were in the same quadrant and walking towards the same quadrant, the subordinate walked towards the dominant and the dominant walked away from the subordinate; this relationship trends towards being more than expected from the within-trial shuffled control for a few seconds before and after time= 0 (peak at time= +1, $r = 1.0000$, $n=5$; $-\log\text{-likelihood} = 2.0561$, *ns*).

7. *No Bait, No Knowledge* controls

In the *No Bait, No Knowledge* controls, the dominant did not follow in the *footsteps* of the subordinate (Figure 5.33), and the subordinate appeared to follow the dominant, though this relationship is not significant (Figure 5.34).

Cross Correlation, Pair 1 *No Bait, No Knowledge*: When Both Chimpanzees are in the Same Quadrant and Walking Towards the Same Quadrant, Does the Dominant Walk Towards the Subordinate, and the Subordinate Walk Away From the Dominant?

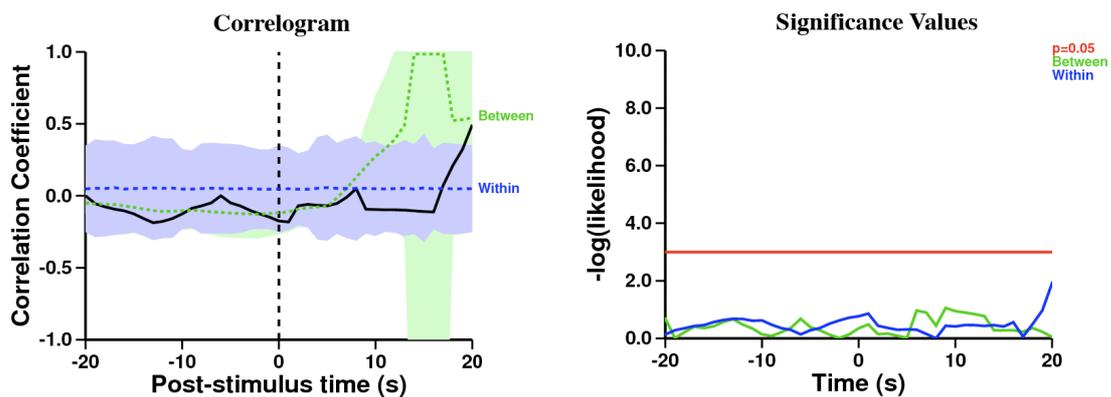


FIGURE 5.33: Referent behaviour: chimpanzees are both in the same quadrant and both walking towards the same quadrant. Target behaviour: dominant walking towards the subordinate and the subordinate walking away from the dominant. After the chimpanzees were in the same quadrant and walking towards the same quadrant, there was no relationship of the dominant walking towards the subordinate and the subordinate walking away from the dominant.

Cross Correlation, Pair 1 *No Bait, No Knowledge*: When Both Chimpanzees are in the Same Quadrant and Walking Towards the Same Quadrant, Does the Subordinate Walk Towards the Dominant, and the Dominant Walk Away From the Subordinate?

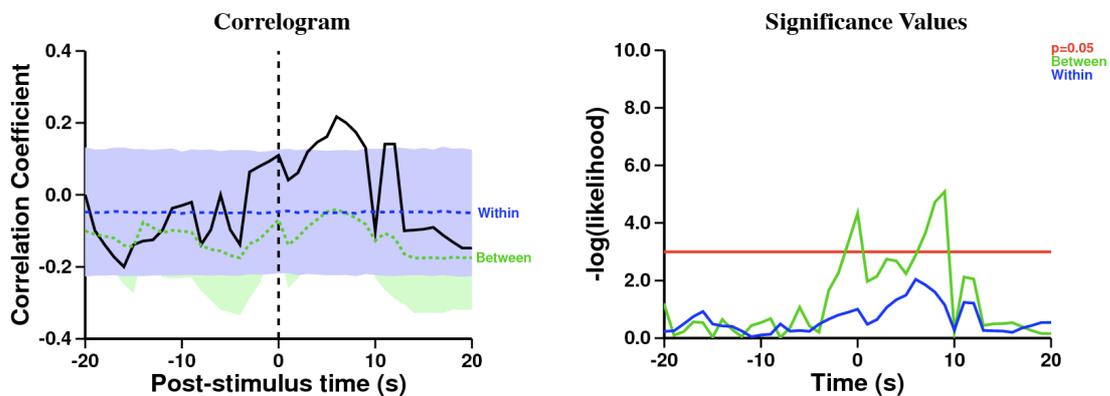


FIGURE 5.34: Referent behaviour: chimpanzees are both in the same quadrant and both walking towards the same quadrant. Target behaviour: subordinate walking towards the dominant and the dominant walking away from the subordinate. After the chimpanzees were in the same quadrant and walking towards the same quadrant, the subordinate walked towards the dominant and the dominant walked away from the subordinate; this relationship trends towards being more than expected from the within-trial shuffled control for a few seconds after time= 0 (peak at time= +6, $r = 0.2173$, $n = 57$; $-\log\text{-likelihood} = 2.0419$, *ns*).

8. Summary of *Footsteps* Behaviour

Where there were differences in knowledge between the two subjects, the dominant was more likely to follow the subordinate than the other way around. At the end of Phase 1, during which time the dominant had not paid much attention to the subordinate's movement, the dominant seemed to realise that the subordinate had privileged information about hidden food, and then the during Phase 2 followed in her *footsteps*. This was an effective strategy to gain information from the subordinate about the food because the subordinate still walked directly to the food without delay, and the dominant was able to take the food on one occasion. However, during Phase 3, when the dominant followed in her *footsteps*, the subordinate changed her tactic by either delaying walking towards the food or walking in an indirect route, and so for Phase 3 overall, the dominant reduced following in the subordinate's *footsteps* as it was no longer an effective exploitative tactic. This pattern was reversed during the *No Knowledge* controls and the *Full Knowledge* controls: the dominant did not follow in the subordinate's *footsteps*, but the subordinate did appear to follow the dominant as the dominant ran to pick up the reward. In the *No Bait, No Knowledge* controls,

the dominant did not follow the subordinate, and the subordinate did follow in the dominant's footsteps.

H. *Convergence*

Again I will describe the patterns of *converging* for the entire dataset, for each of the three distinct phases, and then for the three controls. Since *converging* behaviour is conditional on both chimpanzees being in different quadrants, and both walking towards the same quadrant, there is only one graph per condition; it cannot be determined from the correlogram which chimpanzee initiated the movement. However, considering the result that the dominant walked towards any quadrant after the subordinate had started walking in that direction, one can assume that usually the subordinate initiated a movement trajectory and the dominant *converged* on her movement to walk towards the same destination.

1. Entire *Competition* dataset

A more sophisticated strategy than following in the other's footsteps would be for the dominant to notice the direction of movement of the subordinate, *converge* on her destination, and then walk towards that destination, though it may be from a different starting point or in a different absolute direction of movement from the subordinate. However, the correlogram in Figure 5.35 illustrates that when the two chimpanzees were in different quadrants, they generally did not walk towards the same quadrant.

Cross Correlation, Pair 1 *Competition*: When Both Chimpanzees are in Different Quadrants,
Do They Both Walk Towards the Same Quadrant?

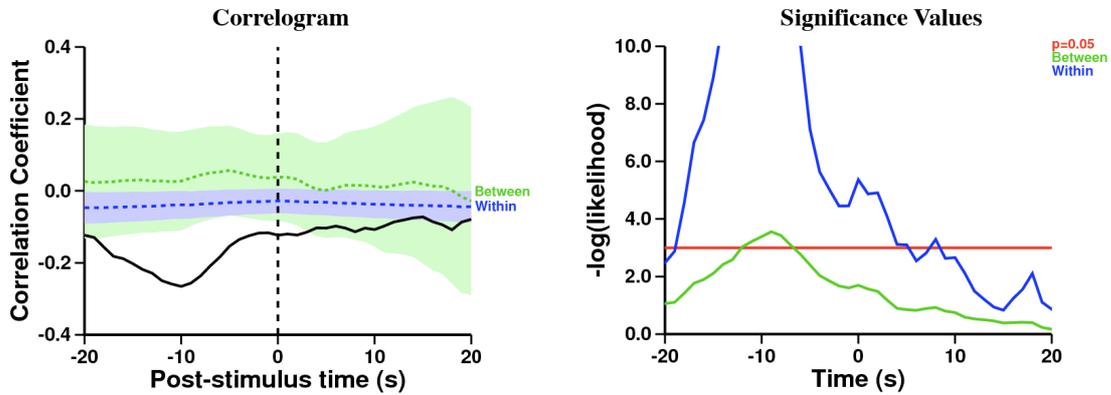


FIGURE 5.35: Referent behaviour: both chimpanzees are in different quadrants. Target behaviour: both chimpanzees walking towards the same quadrant. After the chimpanzees were in different quadrants, both chimpanzees walked towards the same quadrant significantly less than expected from the within-trial shuffled control for a short period but overall there is no relation. While the chimpanzees were in the same quadrant, they walked towards different quadrants (peak at time = -10, $r = -0.2656$, $n = 603$; $-\log\text{-likelihood} = 18.6789$, $p < 0.05$).

2. Phase 1

As with other types of following, *converging* presents different patterns across the three phases. During Phase 1, when the chimpanzees were together in the same quadrant both chimpanzees walked towards the same quadrant significantly more than expected from the within-trial shuffle, but once they were in different quadrants, the relationship was significantly less than expected from the within-trial shuffle (Figure 5.36).

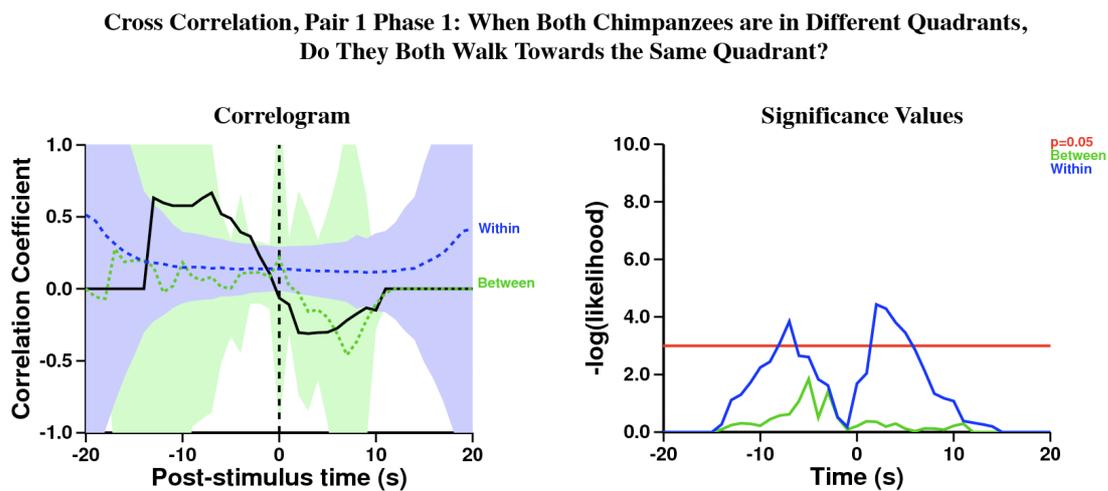


FIGURE 5.36: Referent behaviour: both chimpanzees are in different quadrants. Target behaviour: both chimpanzees walking towards the same quadrant. After the chimpanzees were in different quadrants, both walked towards the same quadrant significantly less than expected from the within-trial shuffled control between time= +2 and +5 (peak at time= +2, $r = -0.3043$, $n = 56$; $-\log\text{-likelihood} = 4.4338$, $p < 0.05$). Furthermore, before the chimpanzees were in different quadrants (before time= 0), they both walked towards the same quadrant significantly more than expected from the within-trial shuffled control (peak at time= -7, $r = 0.6667$, $n = 28$; $-\log\text{-likelihood} = 3.8431$, $p < 0.05$).

3. Phase 2

In Phase 2, the correlation coefficient for *converging* behaviour dips below zero both before and after time= 0 (Figure 5.37). The dip before time= 0 indicates that the chimpanzees are in the same quadrant and walking towards different quadrants, which is logically necessary for the referent behaviour at time= 0 to occur, i.e., when both chimpanzees were in different quadrants. Just before the moment that the chimpanzees were in different quadrants, they appeared to be walking towards the same quadrant, though this relationship was not significant. The dip after time= 0 indicates that the chimpanzees were in different quadrants,

but still walking towards different quadrants. Thus, when they were together in the same quadrant, they walked towards the same quadrant (see Phase 2 *Footsteps*), but when they were in different quadrants, they continued to walk in different directions (see Phase 2 *Approach*).

Cross Correlation, Pair 1 Phase 2: When Both Chimpanzees are in Different Quadrants,
Do They Both Walk Towards the Same Quadrant?

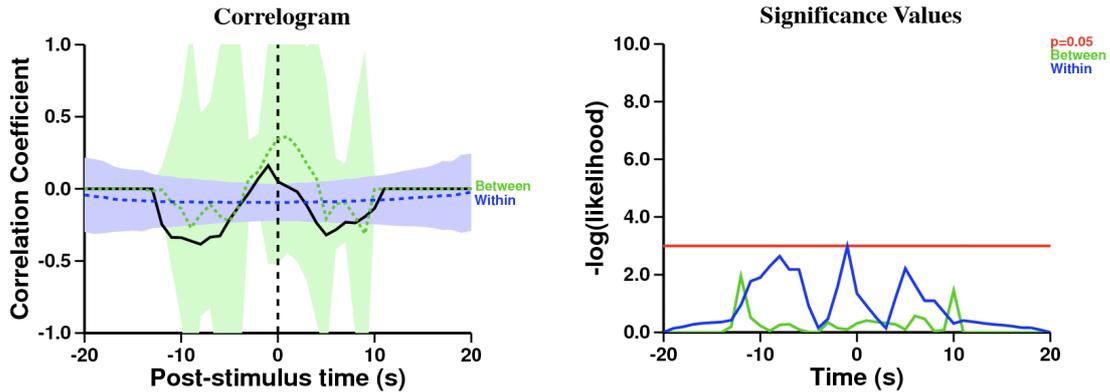


FIGURE 5.37: Referent behaviour: both chimpanzees are in different quadrants. Target behaviour: both chimpanzees walking towards the same quadrant. After the chimpanzees were in different quadrants, both walked towards the same quadrant; this relationship trends towards being more than expected from the within-trial shuffled control at time= -1 (time= -1, $r = 0.1612$, $n = 75$; $-\log\text{-likelihood} = 2.9801$, *ns*). However, both several seconds before and after time= 0, the relationship trends towards being less than expected from the within-trial shuffled control (time= -8, $r = -0.3843$, $n = 41$; $-\log\text{-likelihood} = 2.6406$, *ns*. time= +5, $r = -0.3200$, $n = 54$; $-\log\text{-likelihood} = 2.2132$, *ns*).

Another explanation for the dip after time= 0 in the previous figure could be due to the dominant ceasing her movement altogether. After the chimpanzees were in different quadrants, the dominant stopped walking for five seconds (Figure 5.38).

Cross Correlation, Pair 1 Phase 2: When Both Chimpanzees *Extrapolate*, Does the Dominant Stop Walking?

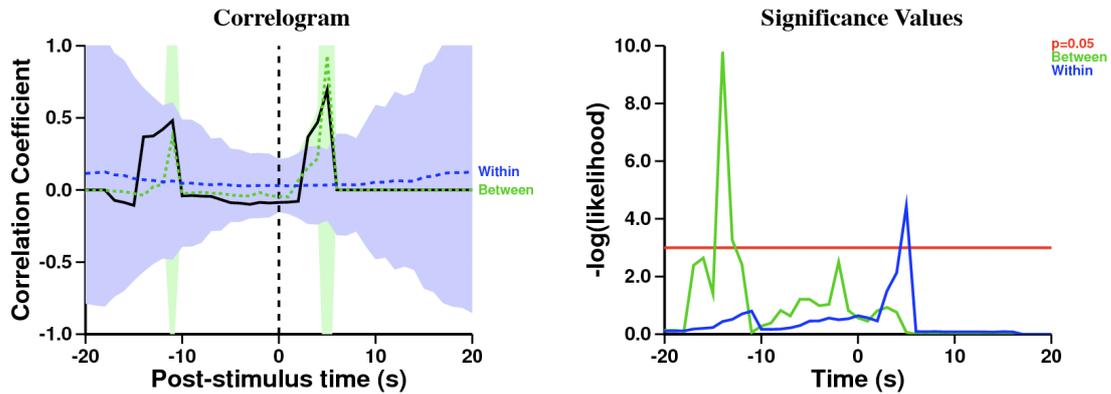


FIGURE 5.38: Referent behaviour: both chimpanzees *converging*. Target behaviour: dominant stops walking for 5 seconds. After both chimpanzees are in different quadrants and walking towards the same quadrant, the dominant stops walking more than expected from the within-trial shuffled control (peak at time= +5, $r = 0.6952$, $n = 31$; $-\log\text{-likelihood} = 4.4364$, $p < 0.05$).

4. Phase 3

The pattern in Phase 3 is similar to the other phases: the chimpanzees did not *converge* (Figure 5.39).

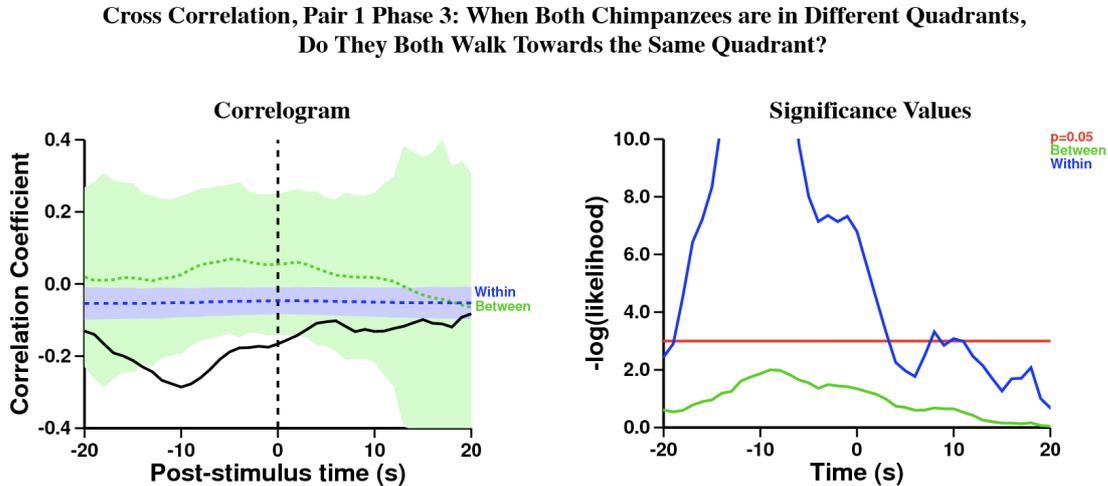


FIGURE 5.39: Referent behaviour: both chimpanzees are in different quadrants. Target behaviour: both chimpanzees walking towards the same quadrant. When the chimpanzees were in the same quadrant, both walked towards the same quadrant significantly less than expected from the within-trial shuffled control (peak at time = -10, $r = -0.2859$, $n = 555$; $-\log$ -likelihood = 18.3077, $p < 0.05$).

There was no evidence from any phase that the chimpanzees used *convergence* as a movement type during the *Competition*. The previous analyses of the other two movement types indicated that only looking at the overall dataset might have hidden certain patterns, so though no differences were found in *convergence*, it was worthwhile to look.

5. No Knowledge controls

While *converging* did not seem to be a common strategy during competitive trials, the chimpanzees did seem to *converge* on each other's destination in the *No Knowledge* controls (Figure 5.40). It was unexpected for either chimpanzee to follow by any definition in the *No Knowledge* controls. As with *approach* behaviour, it could be the case that the dominant preferred to close the distance between herself and the subordinate either in the event that a banana was discovered, or for another reason such as maintaining social cohesion.

**Cross Correlation, Pair 1 *No Knowledge*: When Both Chimpanzees are in Different Quadrants,
Do They Both Walk Towards the Same Quadrant?**

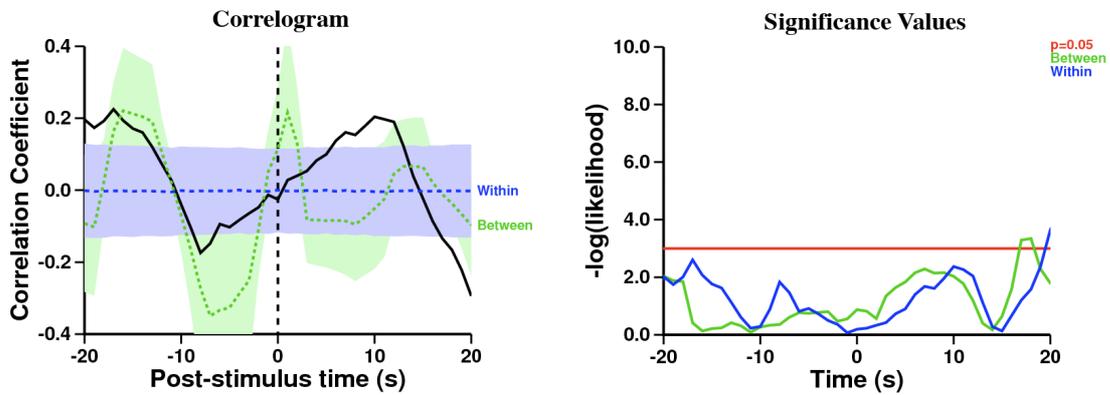


FIGURE 5.40: Referent behaviour: both chimpanzees are in different quadrants. Target behaviour: both chimpanzees walking towards the same quadrant. After the chimpanzees were in different quadrants, both walked towards the same quadrant; this relationship trends towards being more than expected from the within-trial shuffled control (peak at time= +10, $r = 0.2040$, $n = 131$; $-\log\text{-likelihood} = 2.3708$, *ns.*) Many seconds before the chimpanzees were in different quadrants (before time= 0), the chimpanzees were not walking towards the same quadrant; this relationship trends towards being less than expected from the within-trial shuffled control (time= -8, $r = -0.1742$, $n = 137$; $-\log\text{-likelihood} = 1.8307$, *ns.*)

6. Full Knowledge controls

On the other hand, in the *Full Knowledge* controls, the chimpanzees walked towards the same quadrant before they were in different quadrants (Figure 5.41); in the *Full Knowledge* trials, as soon as the dominant entered the quadrant with the hidden banana, the subordinate stopped walking in that direction.

Cross Correlation, Pair 1 *Full Knowledge*: When Both Chimpanzees are in Different Quadrants
Do They Both Walk Towards the Same Quadrant?

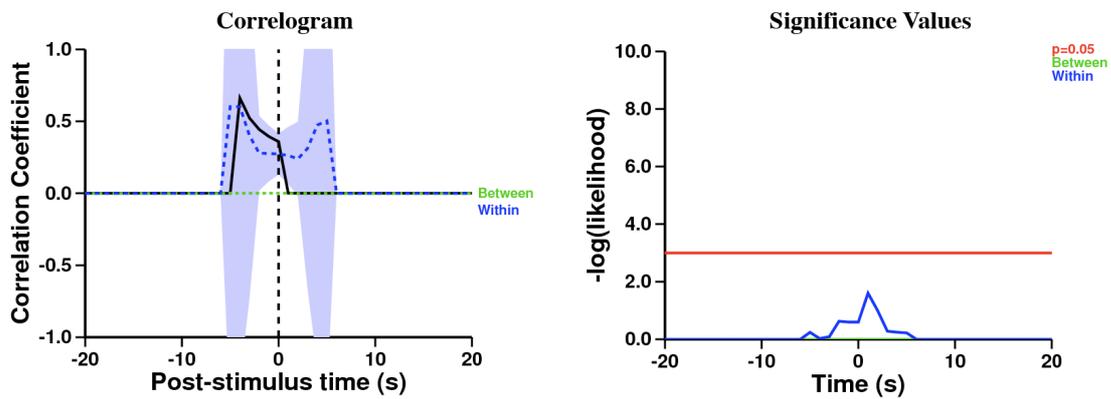


FIGURE 5.41: Referent behaviour: both chimpanzees are in different quadrants. Target behaviour: both chimpanzees walking towards the same quadrant. Before the chimpanzees were in different quadrants, they both walked towards the same quadrant; this relationship trends towards being more than expected from the within-trial shuffled control (time= +1, $r=0.0000$, $n=19$; $-\log\text{-likelihood} = 1.6010$, *ns*).

7. *No Bait, No Knowledge* controls

In the *No Bait, No Knowledge* controls, the chimpanzees did *converge*, but only after spending eleven seconds in different quadrants (Figure 5.42). I did not expect the chimpanzees to follow by any definition during the *No Bait, No Knowledge* controls. Nonetheless, during these trials both chimpanzees spent some time searching, despite the fact that no banana was hidden. It could be the case that the chimpanzees were not aware that there was no reward to be found, or that there was no information to be gained from the other chimpanzee.

Cross Correlation, Pair 1 *No Bait, No Knowledge*: When Both Chimpanzees are in Different Quadrants, Do They Both Walk Towards the Same Quadrant?

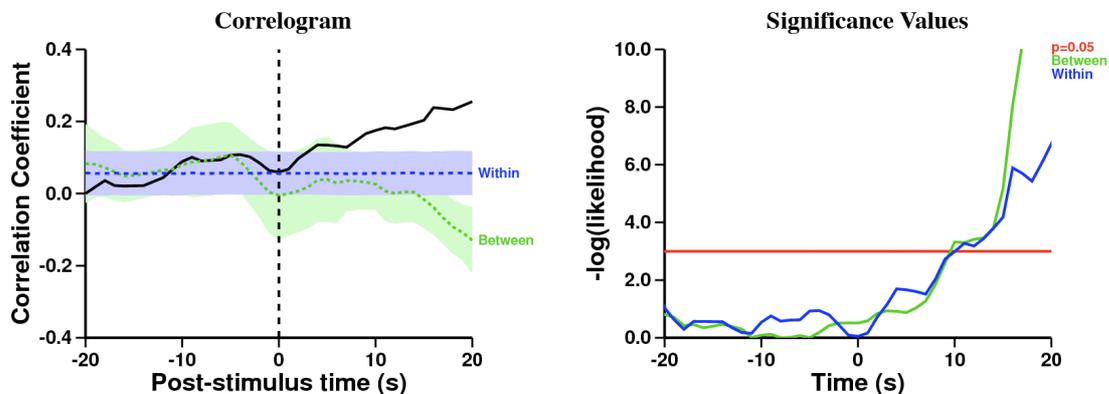


FIGURE 5.42: Referent behaviour: both chimpanzees are in different quadrants. Target behaviour of both chimpanzees walking towards the same quadrant. After the chimpanzees were in different quadrants, both walked towards the same quadrant significantly more than expected from the within-trial shuffled control (peak at time= +20, $r = 0.2551$, $n = 446$; $-\log\text{-likelihood} = 6.7222$, $p < 0.05$).

8. Summary of *Convergence* Behaviour

Unexpectedly, the chimpanzees did not *converge* on each other's destination at a significant level in any phase of the *Competition*. Also unexpectedly, the chimpanzees did *converge* in the *No Knowledge* and *No Bait, No Knowledge* controls, and walked towards the same quadrant before entering different quadrants in the *Full Knowledge* controls.

IV. Discussion, Pair 1

The cross correlation analysis allows me to show the behavioural contingencies that exist between two foraging subjects, as well as changes in their behaviour over time. In the overall *Competition* dataset, after the subordinate started to walk towards the hidden bait, the

dominant walked towards it; it is clear that the dominant adopted the role of scrounger and that her movement towards the hidden bait was motivated by the subordinate's initial movement towards it. It might have been the case that the dominant's behaviour was influenced by the presence of the bait (e.g., an olfactory cue), but I ruled that out by showing that the dominant's movement to three of the four quadrants of their enclosure was also influenced by the subordinate moving in those directions at the same time, regardless of where the bait was hidden.

TABLE 5.4: Overall summary of different following types throughout the experiment, Pair 1 (Results listed in Prediction/Outcome format)

	Overall <i>Competition</i>	Phase 1	Phase 2	Phase 3	<i>No Knowledge</i>	<i>Full Knowledge</i>	<i>No Bait, No Knowledge</i>
Dominant <i>Approaches</i> Subordinate	Yes/Yes	Yes/Yes	Yes/No	Yes/Yes	No/Yes	No/No	No/No
Subordinate <i>Approaches</i> Dominant	No/Yes	No/No	No/No	No/Yes	No/Yes	No/Yes	No/No
Dominant in Subordinate's <i>Footsteps</i>	Yes/No	Yes/No	Yes/Yes	Yes/Yes	No/No	No/No	No/No
Subordinate in Dominant's <i>Footsteps</i>	No/No	No/No	No/No	No/No	No/Yes	No/Yes	No/No
<i>Convergence</i>	Yes/No	Yes/No	Yes/No	Yes/No	No/Yes	Yes/Yes	No/Yes

I examined following behaviour, looking at three different definitions: *approach*, walking in the other's *footsteps*, and *converging* on the other's destination (Table 5.4 summarises the result of each movement analysis for each experimental condition). While previous studies described "following," they did not differentiate between different types of following as I have done here (Leca et al., 2003; Meunier et al., 2008; Sueur & Petit, 2008, 2010; though see Stueckle & Zinner, 2008, for "leading from the back"). During data collection as well as the initial stages of operationalising a definition for "following," it appeared that one definition would not encompass the variety of actions I witnessed. It seemed that for the dominant to walk towards the subordinate by *approaching* was not only very different from coordinating her movement to walk in the subordinate's *footsteps*, but also less sophisticated than taking the subordinate's perspective and adjusting her own movement to *converge* on the subordinate's destination.

The cross correlations showed that for all phases of the *Competition*, the dominant moved to be closer to the subordinate more than the subordinate moved to be closer to the dominant: the dominant *approached* the subordinate in Phases 1 and 3, and followed in the subordinate's *footsteps* in Phase 2, whereas the subordinate only started to *approach* the dominant in the third phase of the experiment. This indicates that the dominant adjusted her movement to get physically closer to the subordinate, but there was no evidence from the *Competition* to support the hypothesis that the dominant *converged* with the subordinate's movement in order to adjust her own walking to arrive at the same destination.

The results show that, as expected, it took several trials before the dominant started to exhibit any following behaviour (she started searching for the bait on the eighth of 24 *Competition* trials). During Phase 1, the subordinate walked directly to the bait and therefore did not direct any following behaviour to the dominant; the dominant had not yet learned that the subordinate had knowledge of a hidden banana. The dominant very briefly *approached* the subordinate, usually taking only a few steps from her position on the central climbing platform, but did not exploit the subordinate's foraging success.

During Phase 2, the dominant started to pay more attention to the subordinate's movement and increased her exploitation of the subordinate by following in her *footsteps*, and she gained a banana on one trial. However, when the chimpanzees were in different quadrants the dominant no longer *approached* or *converged*. By maintaining a short distance between herself and the subordinate, the dominant was able to successfully exploit the subordinate's foraging success on trial 11. As with the previous phase, in this phase the subordinate did not direct any following behaviour towards the dominant.

By the third phase, the dominant picked up the banana more frequently and so the subordinate changed her behaviour to avoid walking directly to the bait: when the dominant *approached*, the subordinate stopped walking. In Phase 3, the subordinate delayed walking to the hidden food on four trials and walked away from where the food was hidden on one trial, which functioned to mislead the dominant. Therefore, the dominant's previous tactic of exploitation by following in the subordinate's *footsteps* was no longer successful. There was a trend in the data showing the dominant following in the subordinate's *footsteps*, but much less than before. The dominant no longer followed very closely (within the same quadrant) and instead used the tactic of *approaching* the subordinate. The subordinate also *approached* the dominant, which could have been during the cases in which the subordinate found the bait

but then abandoned it: she may have *approached* the dominant as she walked away from the bait's location, and the later timing of the peak in the correlogram supports this.

The *No Knowledge* control trials presented different patterns for each type of following. I did not expect to see any type of following, since neither chimpanzee saw the baiting procedure (where before the dominant could see through the mesh adjoining their cages that the subordinate was looking through her window outside to the enclosure as the experimenter hid the bait). However, the dominant continued to *approach* the subordinate, and this tactic may have been maintained because the subordinate did happen to find a banana on one trial, and the dominant may have been motivated to continue using this tactic. The subordinate also *approached* the dominant, and it is possible that this was to maintain social cohesion and reduce the distance between herself and her opponent. However, during the *No Knowledge* trials, the order of following in *footsteps* was reversed compared to experimental trials in Phases 2 and 3: the subordinate followed the dominant. This can be explained by the fact that the dominant entered the enclosure before the subordinate, and so the subordinate must walk in the dominant's *footsteps* for a brief period at the start of each trial. Similarly, the chimpanzees *converged* on each other's destinations in the *No Knowledge* controls, the opposite of the experimental trials. These different results suggest that when the subordinate did not have knowledge about where the food was hidden, the dominant did not closely follow the subordinate, for example she did not follow in her *footsteps*. Her continued *approaching* and *converging* behaviour may be attributed to the fact that the dominant had learned over many trials that those were successful strategies to take advantage of the subordinate, and four control trials did not sufficiently reduce those types of exploitation.

I also found different results from the *Competition* trials in the *Full Knowledge* control. Based on results from previous studies (Coussi-Korbel, 1994; Hare et al., 2000, 2001; Karin-D'Arcy & Povinelli, 2002; Bräuer, et al., 2007), I expected that the dominant would not rely on the subordinate for any movement cue when she had information of her own about the hidden banana. The results are consistent with previous studies: the dominant obtained a larger proportion of bananas than the subordinate, and did not *approach*, walk in the *footsteps* of, or *converge* on the subordinate's destination, whereas the subordinate did follow in the dominant's *footsteps*. The subordinate's following could be an artefact of the dominant running to retrieve the reward faster than the subordinate, making it appear as if the

subordinate was following the dominant, though it is doubtful that the subordinate followed in order to gain information from the dominant.

The *No Bait, No Knowledge* controls were implemented to determine if the dominant would continue to approach the subordinate when no banana was hidden in the enclosure. While she did not *approach* as she had done in the original *No Knowledge* controls, she did *converge*, and the subordinate briefly followed in the dominant's *footsteps*. It could be the case that the chimpanzees learned over numerous trials that a banana was usually hidden in the enclosure, and that searching despite not knowing its location could be a useful strategy, as in the *No Knowledge* controls. Additionally, though a banana was not hidden, an experimenter did enter the enclosure as if to hide something, so the chimpanzees may have searched because they had made the association between researchers in the enclosure and hidden food items.

V. Results: Pair 2, Reinette and Georgia

Now I will repeat the same analyses for the second pair of chimpanzees, subordinate Reinette and dominant Georgia, to test the ideas that were developed with the first pair. The comparison of both pairs will demonstrate that there are chimpanzee-typical exploitation and resistance behaviours, but also that different individuals employed these movement types quite differently. A narration of their behaviour will give the impression that the dominant eagerly searched the enclosure and that the subordinate was hesitant to approach the location of the hidden food from the very beginning of the *Competition*. The dominant reduced her use of all three following types by the end as the subordinate alternated between delaying and walking immediately to the hidden bait. The correlograms analysing the data between the three phases will bear out this trend, and will provide answers to the questions asked above, such as, did the dominant *approach/footsteps/converge* the subordinate (and did the subordinate use these movement types to follow the dominant)?

A. Who Found the Reward?

The subordinate, Reinette, was informed of the location of the hidden food in the *Competition* trials, and ultimately obtained 15 of 24 bananas (62.5%). Georgia, the ignorant dominant, obtained the banana on the other nine trials (37.5%), indicating that she represented a high level of exploitation pressure upon Reinette. When neither subject knew where the banana was hidden in the *No Knowledge* controls, the subordinate found the

banana on one of four trials, the dominant found the banana on two trials, and neither chimpanzee found the bait on the remaining trial. In the *Full Knowledge* condition, the dominant found all four bananas. No bananas were hidden in the *No Bait, No Knowledge* controls (Figure 5.43). From this initial glance at the overall percentage of food won by each subject, we have learned that when an individual had seen where a reward was hidden, she was more likely to find it than when she had not seen it hidden—though searching through familiar locations can certainly increase a subject’s chances of finding a bait that she had not seen.

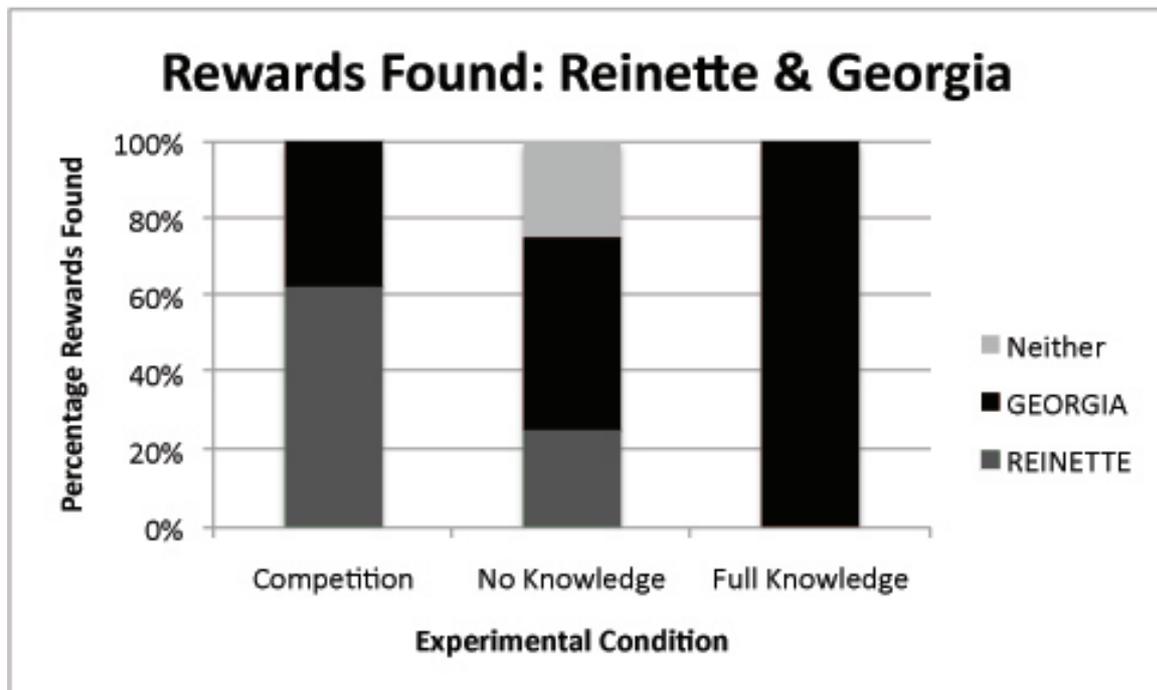


FIGURE 5.43: Percent rewards found by each subject, per condition, Pair 2

B. Descriptive Account of *Competition*

Figure 5.44 shows the pattern of food retrieval: the dominant won on the first trial, but then the subordinate won for seven consecutive trials. After this, the dominant and subordinate alternated in finding the banana on every other trial.

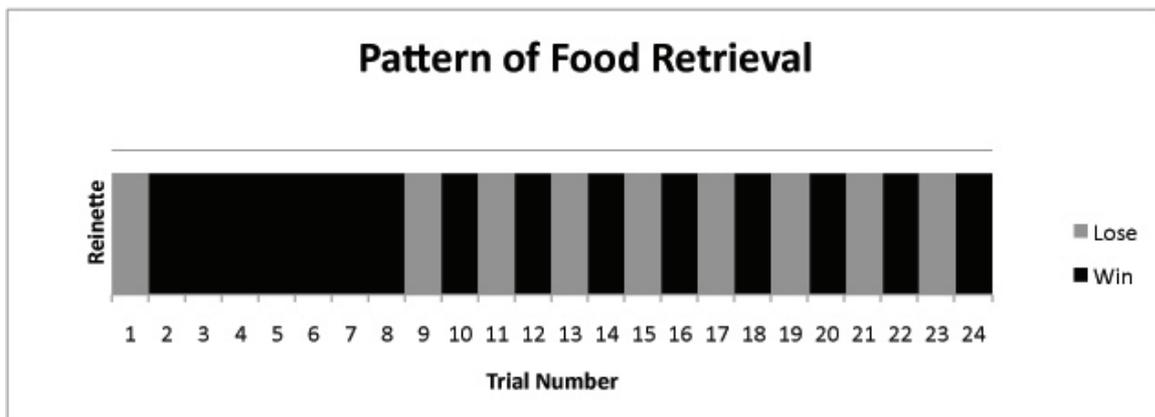


FIGURE 5.44: Pattern of the Subordinate’s Food Retrieval, Pair 2

The dataset was divided into three phases based on changes in either subject’s tactics. During Phase 1 (trials 1-11), the subordinate avoided walking directly to the hidden bait and paused frequently while the dominant searched. During Phase 2 (trials 12-16), the subordinate walked directly to the bait, while the dominant continued to search. During Phase 3 (trials 17-24), the subordinate alternated tactics between walking directly and delaying her approach to the food, and she lost the reward to the dominant on every other trial.

Overall, the mean trial length for the *Competition* was 38 seconds (Figure 5.45). When no bait was found, the trial was terminated at 300 seconds (this affects the *No Knowledge*, and *No Bait, No Knowledge* conditions, as well as the final trial in Phase 3 of the *Competition* and one trial in the *Full Knowledge* condition). The mean trial length for the *No Knowledge* condition was 97.5 seconds, 19.5 seconds for *Full Knowledge*, and 300 seconds for *No Bait, No Knowledge*. An ANOVA tested the differences in mean trial time and found a significant difference between conditions ($F= 36.41$, $df= 39$, $p < 0.01$).

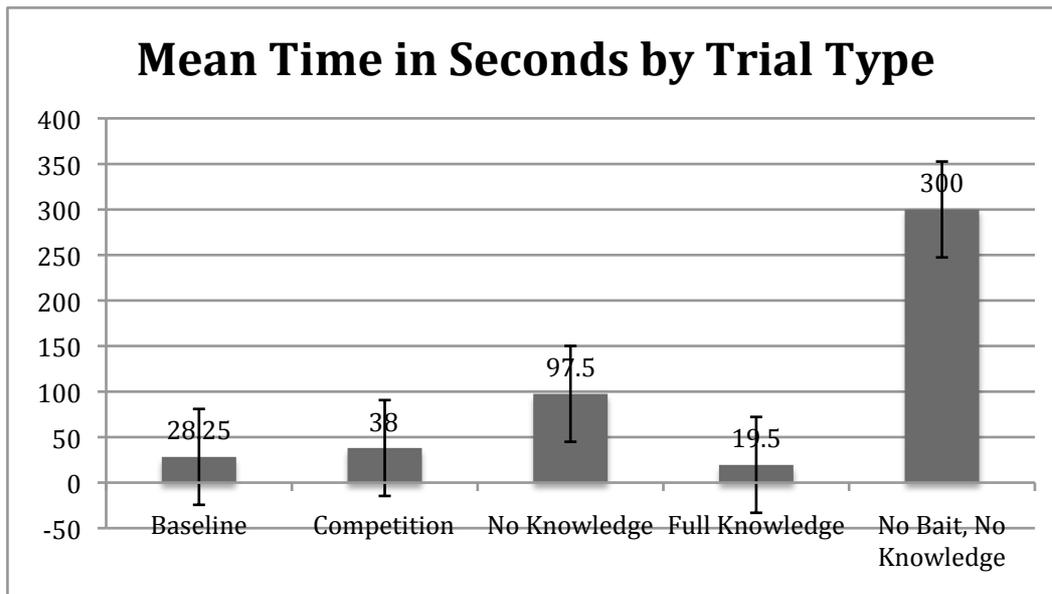


FIGURE 5.45: Mean trial time with standard error, per condition (no banana was hidden in the final *No Bait, No Knowledge* condition), Pair 2

As the dominant's movement and search tactics changed, so did the subordinate's; this is reflected in the mean trial time, which changed over the three phases as the subordinate avoided walking directly to the bait. The mean trial length during Phase 1 was 40.45 seconds; the mean trial length during Phase 2 was 35.4 seconds; the mean trial length in Phase 3 was 36.25 seconds. An ANOVA tested the differences in mean trial time and no significant difference was found between the phases ($F = 0.2170$, $df = 23$, $p = 0.807$).

1. Phase 1: Trials 1-11

On the first trial of the experiment, the subordinate walked in a zigzag pattern and did not walk directly towards the food. The ignorant dominant followed the knowledgeable subordinate for a few paces before passing in front of her. The dominant frequently looked back to the subordinate and adjusted her own direction of movement to match the subordinate's. Eventually the dominant found the bait. On the second trial, the dominant walked towards the subordinate, but when the dominant paused briefly, the subordinate ran ahead to pick up the reward. On the third trial, the subordinate sat and waited for 9 seconds as the dominant passed by where the bait was hidden. The subordinate approached the hiding location and again waited for 4 seconds until the dominant walked away and was no longer looking at her before she uncovered the banana. On the fourth trial, the dominant was searching when she turned around and noticed the subordinate's direction of movement, and changed her own direction of movement to walk towards the subordinate. The subordinate

paused in her path for 4 seconds until the dominant was busy searching again at another location before the subordinate continued towards the hiding location and picked up the banana. This pattern of waiting until the dominant was busy searching elsewhere echoes a narrative from Coussi-Korbel, “As soon as Boss [the ignorant dominant] was engaged in his search, Rapide [the informed subordinate] gave Boss a final glance, moved out of the nonprovisioned zone, and set out in a straight line for the food” (Coussi-Korbel, 1994, p. 169). On the fifth trial the dominant saw that the subordinate started climbing the structure in the centre of the enclosure, and rushed to climb it as well, but the subordinate still managed to pick up the food reward that was hidden there first. The dominant followed the subordinate closely on the next trial, and so the subordinate took an indirect route to the reward, and the dominant stopped following after a short time. On the next two trials, the subordinate sat and waited until the dominant was not close to the bait before going to pick it up. The dominant found the bait on trial 9. On the next trial, the subordinate again took an indirect route to the reward as the dominant followed her closely, ran ahead of her, waited, and followed again; in this case the subordinate was able to find the reward before the dominant. The dominant won again on the next trial. The dominant’s frequent glances towards the subordinate coupled with her changing her direction of movement to match the subordinate’s gave the impression that the dominant used the subordinate’s movement cues to direct her own search.

2. Phase 2: Trials 12-16

During the second phase the dominant continued to search for the reward but did not follow the subordinate as closely as during the first phase. The subordinate took the opportunity to run to retrieve the food reward on two occasions, and walked directly to the food on a third. On the two trials in which the subordinate paused or took an indirect route towards the bait, the dominant found the bait in her random searching before the subordinate could reach it. One should ask whether the subordinate’s new tactic of running directly to the reward in this phase was due to the dominant’s lack of interest, and therefore a reduced level of exploitation on the subordinate, or a tactic to cope with the dominant’s exploitation.

3. Phase 3: Trials 17-24

During the third phase, the subordinate alternated tactics between walking directly to the bait, and delaying her approach to the location where the banana was hidden. The dominant often adjusted her own direction of movement to match the subordinate’s direction, and on several occasions walked ahead of the subordinate and found the reward. The

subordinate was successful on the trials in which she walked directly to the reward. On trial 17, the subordinate was walking towards the bait but hesitated when the dominant was close, and lost the reward to the dominant, who had been searching ahead of the subordinate. The subordinate walked directly to the reward on the next trial, and the dominant followed her closely, but did not run ahead or take the reward. On trial 19, the subordinate came outside and immediately sat down and waited as the dominant searched, and the dominant quickly found the hidden banana. On trial 20, the subordinate walked directly to the reward, and the dominant did not follow her. Overall, it seemed that the dominant would follow the subordinate for a few steps before running ahead of her in order to exploit her, and on some occasions used a “‘quick search’ strategy” (i.e., searching quickly through numerous locations before the subordinate arrived: Hirata & Matsuzawa, 2001, p. 291).

4. *No Knowledge* controls

On the first *No Knowledge* control trial, both chimpanzees were very eager to search for the banana, though neither had seen where it was hidden: the dominant searched in ten locations, and the subordinate searched three, though neither found the hidden banana. On the second trial, the subordinate found the banana while searching in her second location; the dominant had searched four locations and continued to search in three more locations as both chimpanzees walked around the perimeter of the enclosure twice. On the following trial, the dominant found the bait on her third search, and the subordinate had searched one other location. Neither chimpanzee continued to search afterward. The dominant again found the reward on the final trial, and both chimpanzees searched both before and after the reward had been eaten.

5. Phase 3 continued

After the four *No Knowledge* control trials, the *Competition* resumed. On trial 21, the dominant walked ahead of the subordinate and found the banana. On the next trial, the subordinate walked directly to the reward and picked it up without the dominant following her. On trial 23, the dominant found the reward before the subordinate came outside. On the last trial, the subordinate remained inside for a short while and as soon as she entered the enclosure, the dominant walked towards the same quadrant as the subordinate. The subordinate immediately turned around to return inside. While the dominant was busy searching on the opposite side of the enclosure, the subordinate again entered the enclosure and walked directly to the reward. On many trials in Phase 3 it seemed that the dominant

managed to obtain the banana because the subordinate ‘revealed some cue to her,’ whether by walking towards the reward, glancing nervously towards the dominant as she walked, or hesitating to act as the dominant searched close to where the food was hidden. Yet how does one differentiate between these cues to determine which, or which combination, had the greatest effect on whether the dominant approached the location of the hidden food?

6. Full Knowledge controls

On all four *Full Knowledge* controls, the dominant ran directly to the food reward, often reaching it before the subordinate had taken more than a few steps into the enclosure.

7. No Bait, No Knowledge controls

Both chimpanzees continued to search on every trial of the *No Bait, No Knowledge* controls, and the dominant especially made a great search effort and occasionally checked back in the same locations numerous times. On the first trial, the dominant searched fifteen times total, and the subordinate searched five. Towards the end of the trial both chimpanzees picked up a handful of chow that was in their enclosure, and sat down on the climbing structure to eat it. At the beginning of the second trial, the subordinate sat down for 45 seconds before moving to another location and sitting for 47 seconds; at 2:42, she laid down on the climbing structure and remained there for the rest of the 5-minute trial. The dominant joined her at 3:16 minutes into the trial and sat down next to her. The subordinate did not search on that trial, and the dominant searched in five locations. On the third trial the dominant searched eight times, and the subordinate searched twice, before both returned inside to the ‘Cognition Room’ by 2:20, where they stayed the remainder of the trial. On the last trial, the dominant searched in twelve locations, and the subordinate searched in one.

8. Summary

Over the course of the *Competition*, it appeared that the subordinate alternated tactics in order to avoid the dominant’s exploitation, with limited success. The dominant often followed the subordinate closely, then walked ahead of her and expanded her search area. The dominant frequently looked back to the subordinate and adjusted her own movement to match the subordinate’s direction of movement. The dominant often found the banana when the subordinate hesitated to approach the hiding place, and somehow the dominant was able to use movement cues from the subordinate in order to find the food reward on several trials.

As mentioned previously, Menzel described the “continuous feedback between leaders and followers,” (p. 134), and while I have attempted to relate a similar story, the

narration itself is not sufficient evidence of continuous feedback or of any other relationship. Many analyses of this experimental paradigm in prior publications struggled to show statistically what observers so easily see during interactions between subjects. Cross correlations will again be used to show how each subject's behaviour changed throughout the course of the experiment, and examine whether real behavioural contingencies existed between the subjects.

C. Analysis of Walking Towards the Bait During *Competition*

Here I will use cross correlations to address the subjects' movement towards the hidden bait; as shown in Figures 5.45 and 5.46, the dominant did retrieve the bait on nearly 40% of the trials—but how did she arrive at the hiding place? It is possible that the dominant was able to find the bait by searching randomly, by using an olfactory cue, or by using a movement cue given by the knowledgeable subordinate. I address the hypothesis that the dominant uses the subordinate's movement to guide her own by asking, "When the subordinate walks towards the bait, does the dominant walk towards the bait?" (Figure 5.48; graphs for *No Knowledge* and *Full Knowledge* controls are included in the appendix to Chapter 5, figures 5.3 and 5.4).

There is no significant relationship between the dominant and subordinate walking towards the bait (Figure 5.46). The dominant did not seem to rely on the subordinate first walking towards the bait in order to find it. When the reverse situation is analysed (i.e., whether the subordinate walks towards the bait after the dominant starts walking towards it), there is still no relationship (Figure 5.47).

**Cross Correlation, Pair 2 Competition: When the Subordinate Walks Towards the Bait,
Does the Dominant Walk Towards the Bait?**

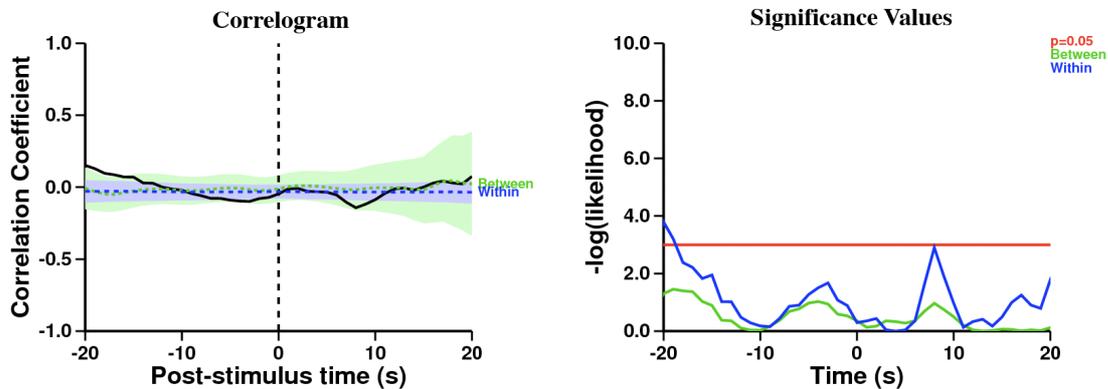


FIGURE 5.46: Referent behaviour: subordinate walking towards the bait. Target behaviour: dominant walking towards the bait. After the subordinate walked towards the bait, there was no relationship with the dominant also walking towards the bait, though the relationship trends towards being less than expected from the within-trial shuffle, indicating that the dominant did not walk towards the bait when the subordinate did (time= +8, $r = -0.1431$, $n = 234$; $-\log\text{-likelihood} = 2.8975$, *ns*).

**Cross Correlation, Pair 2 Competition: When the Dominant Walks Towards the Bait,
Does the Subordinate Walk Towards the Bait?**

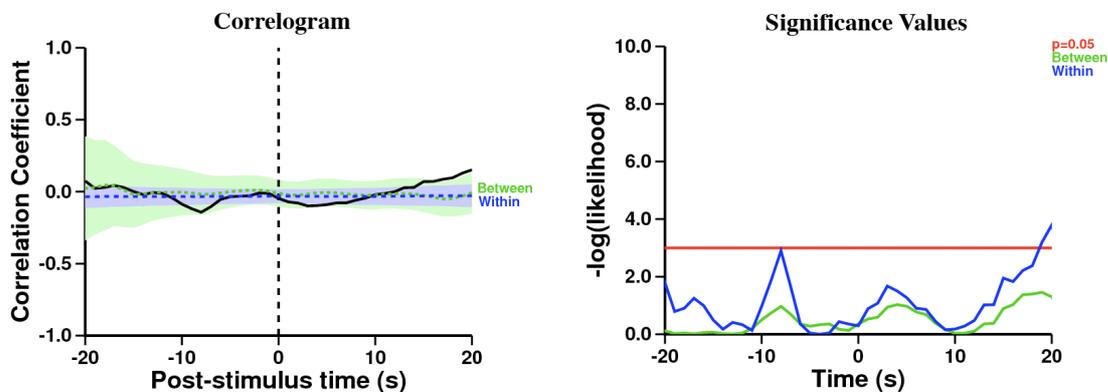


FIGURE 5.47: Referent behaviour: dominant walking towards the bait. Target behaviour: subordinate walking towards the bait. After the dominant walked towards the bait, there was no relationship with the subordinate walking towards the bait. This data is the same as in Figure 5.3: the cross correlation with the referent and target swapped results in a graph that is reversed in time along the x-axis.

Though the dominant did not seem to rely on the subordinate's movement cue towards the bait in order to find it, perhaps the dominant can find the bait using a different cue, e.g., an olfactory cue. Do the chimpanzees walk together towards other areas of the

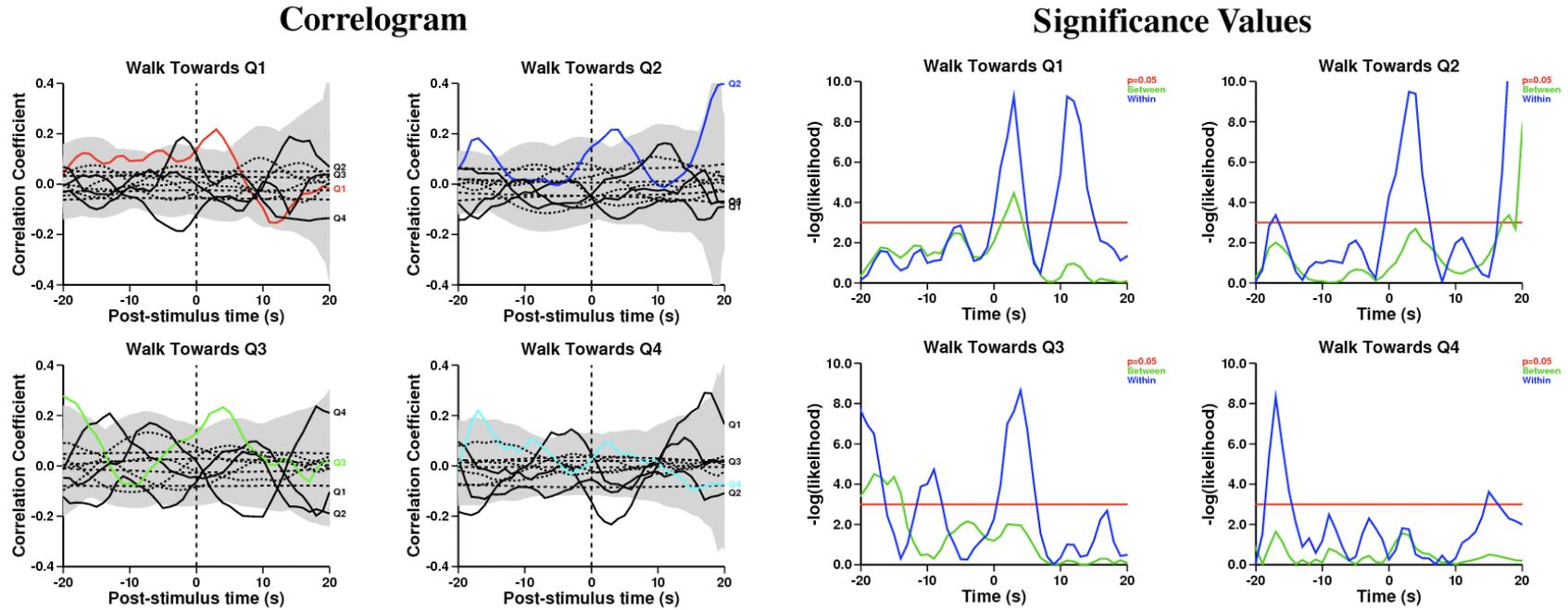
enclosure, regardless of the location of the bait? Because of these concerns, I analysed the chimpanzees' movements by investigating whether they both walked towards the same absolute quadrant of the enclosure, regardless of the location of the bait.

D. Analysis of Walking Towards Absolute Directions During *Competition*

To address the chimpanzees' movement towards the four quadrants in their enclosure I asked, "When the subordinate walks towards a quadrant, towards which quadrant does the dominant walk?" I compared the subordinate's movement towards one quadrant with the dominant's likelihood of walking towards any of the four quadrants (Figure 5.48). It appears that whether the dominant moved towards a particular quadrant was dependent on a cue from the subordinate moving in that direction first. When the subordinate walked towards three of the four quadrants, the correlation coefficient of the dominant walking towards the *same quadrant* as the subordinate, rather than any other quadrant, trends towards significance when compared to the between-trial shuffled control. This particular control is used because the data are coded in absolute terms (i.e., towards quadrants 1, 2, 3, 4): the chimpanzees were in a differently numbered quadrant on each trial, so shuffling between trials eliminated contingent relationships but maintained sequences of behaviour (see Chapter 4: Statistical Methods). This shows that both chimpanzees behaved towards the same absolute direction at the same time, when the location of the bait was not taken into account. However, it is clear that there is a stronger influence of walking towards Q1 and Q2: the significance values for both chimpanzees walking in those directions are much higher than for other quadrants, and this may be explained by the layout of the enclosure as discussed in the following section.

FIGURE 5.48 (next page): In each panel, the referent behaviour at time= 0 is the subordinate walking towards the quadrant of that panel. The coloured line in each panel represents the cross correlation of the dominant walking towards the same quadrant as the subordinate. The three solid black lines represent the cross correlation of the dominant walking towards each of the other three quadrants. The dotted lines with the gray spread represent the within- and between-trial shuffled controls and their standard errors of the mean. For example, in the top left panel, the referent behaviour at time= 0 is the subordinate walking towards Q1 and it is correlated with the target behaviour of the dominant walking towards Q1, and this relationship is plotted with a red line. The black lines show the cross correlations of the subordinate walking towards Q1 with the dominant walking towards Q2, Q3, and Q4. When the subordinate walked towards Q1 (time= +3, $r = 0.2180$, $n = 502$; $-\log\text{-likelihood} = 4.4565$, $p < 0.05$), Q2 (time= +4, $r = 0.2164$, $n = 478$; $-\log\text{-likelihood} = 2.6906$, ns), and Q3 (time= +2, $r = 0.2069$, $n = 524$; $-\log\text{-likelihood} = 2.0093$, ns), the dominant walked towards the same quadrant as the subordinate; this relationship trends towards being more than expected from the between-trial shuffled control. When the subordinate walked towards Q4, there was no relationship of the dominant walking towards Q4 (time= +2, $r = 0.0898$, $n = 524$; $-\log\text{-likelihood} = 1.5588$, ns).

Cross Correlations, Pair 2 *Competition*: When the Subordinate Walks Towards a Quadrant, Towards Which Quadrant Does the Dominant Walk?



There was a larger effect of both chimpanzees walking towards Quadrants 1 and 2, so I analysed how much time each chimpanzee spent currently in, and walking towards, each quadrant in the enclosure to determine if these results were artefacts due to the experimental setup.

E. Time Spent in Each Quadrant During *Competition*

The chimpanzees' enclosure is divided into four approximately equal quadrants. The chimpanzees were released from cages in the 'Cognition Room' at the base of Q3. Given the spatial layout of the enclosure, there were differences in the amount of time subjects spent in each quadrant: Quadrant 2 is the farthest from the start position in Q3, and it naturally takes more time to travel to Q2 than to either Q1 or Q4. Additionally, subjects seemed to spend less time overall in areas farther away from their start cages, especially Q2. Table 5.5 lists the percentage of time that each subject in this pair spent *currently in* each quadrant, and Table 5.6 lists the percentage of time each spent *moving towards* each quadrant.

A one-way chi-square goodness of fit tested the null hypothesis that each subject entered each quadrant an equal number of times; whereas Reinette entered each quadrant an equal number of times (3, $n=28$), $\chi^2=0.86$, ns , Georgia showed significant differences in her pattern of entering different areas of the enclosure (3, $n=39$), $\chi^2=10.54$, $p=0.0145$.

TABLE 5.5: Percent of time each subject spends currently in each quadrant, Pair 2

Quadrant	Reinette Current	Georgia Current
Q1	7.59%	25.30%
Q2	8.20%	1.35%
Q3	64.24%	62.99%
Q4	19.97%	10.36%

TABLE 5.6: Percent of time each subject spends moving towards each quadrant, Pair 2

Quadrant	Reinette Direction	Georgia Direction
Q1	15.94%	30.28%
Q2	20.74%	10.63%
Q3	21.05%	12.25%
Q4	23.68%	20.59%
0 (No Locomotion)	18.58%	26.25%

Similarly, the distribution of time that the pair spent together in the same quadrant is quite different for each location (Table 5.7). Overall, when both subjects were outside (62.06% of all trials), they were both in the same quadrant 66.43% of the time. Of this total

time spent together, they spent the majority of their time, 78.99%, in Quadrant 3. Of the total time spent together, 10.1% is in Quadrant 1. There appears to be a side bias towards the left side of the enclosure (Quadrants 1 and 3), as they only spent time in Quadrants 2 and 4 for 2.13% and 8.78% of the time they were together in the same quadrant, respectively.

TABLE 5.7: Percent of time spent together in each quadrant, of the overall time spent together outside, Pair 2

Quadrant	Time
Q1	10.10%
Q2	2.13%
Q3	78.99%
Q4	8.78%

When analysed in terms of relative position in the enclosure (e.g., towards the bait), the chimpanzees did not seem to walk together: however, when analysed in terms of absolute direction (e.g., towards Q2), both subjects walked together upon the subordinate's movement cue at time= 0, with the exception of towards Q4 for which there did not seem to be any relationship. Overall, the general pattern of walking towards the same direction at the same time may indicate that the ignorant dominant was following the knowledgeable subordinate in order to exploit her foraging success.

On the surface, both chimpanzees were walking towards the same quadrant at the same time, but there were subtler interactions occurring that are not portrayed by those graphs: the dominant may be acting in distinct ways such as *approaching* the subordinate's current location, following in her *footsteps*, or *converging* on her destination. Furthermore, these strategies may differ over the course of the *Competition*; the dominant may change tactics as her foraging success changes, based on the subordinate's movements.

F. Approach

I will describe the patterns of *approaching* through the entire dataset by first asking whether the dominant *approached* the subordinate, and secondly whether the subordinate *approached* the dominant. Recall that *approach* is defined as "the subjects are in different quadrants of the enclosure and one individual walks towards the other." Then I will break down the analyses and ask these questions for each of the three distinct phases in order to illustrate any changes in either subject's actions. Then I will present graphs for the *No Knowledge*, *Full Knowledge*, and *No Bait, No Knowledge* conditions.

1. Entire *Competition* dataset

For the entire *Competition* dataset, at the moment that the chimpanzees were in different quadrants, neither the dominant nor the subordinate *approached* her opponent, and this relationship was significantly less than expected from the within-trial shuffled control. This particular control is used because the data are collapsed (same/different quadrant, rather than quadrants 1, 2, 3, 4): because the chimpanzees being in “different” quadrants on trial one does not necessarily connote the same physical places as when they are in “different” quadrants on trial two, a within-trial shuffle is more appropriate because it maintains the behavioural contingencies between subjects but eliminates the sequences of behaviour (see Chapter 4: Statistical Methods). Many seconds later, both chimpanzees did *approach* her opponent significantly more than expected compared to the within-trial shuffled control (Figures 5.49 and 5.50).

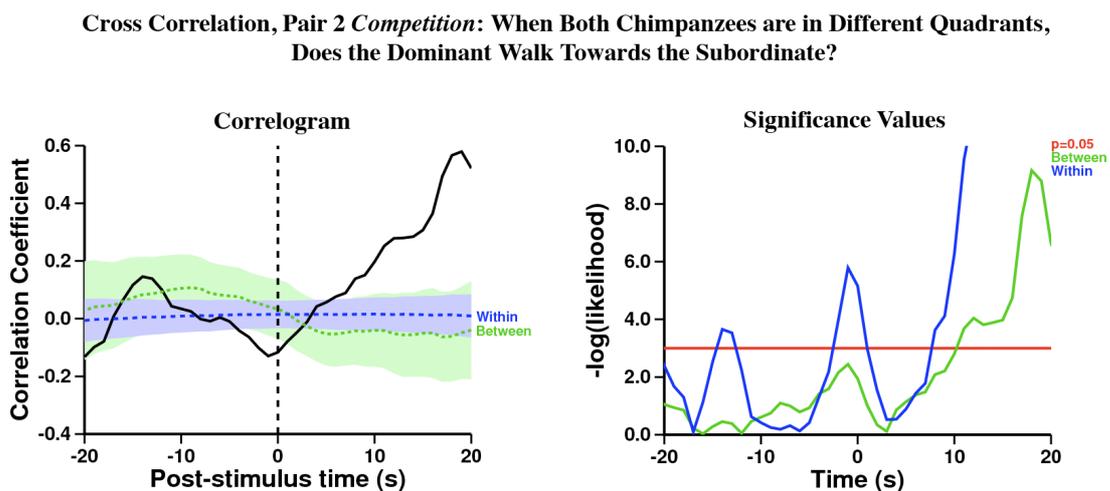


FIGURE 5.49: Referent behaviour: both chimpanzees are in different quadrants. Target behaviour: dominant walking towards the subordinate. Just before, and at the moment that the chimpanzees were in different quadrants, the dominant walked towards the subordinate significantly less than expected from the within-trial shuffled control (peak at time= -1, $r = -0.1297$, $n = 412$; $-\log\text{-likelihood} = 5.7895$, $p < 0.05$). After the chimpanzees were in different quadrants for a few seconds, the dominant walked towards the subordinate significantly more than expected (peak at time= +18, $r = 0.5664$, $n = 123$; $-\log\text{-likelihood} = 26.9548$, $p < 0.05$). Also, when the chimpanzees were in the same quadrant (before time= 0), the dominant walked towards the subordinate significantly more than expected (peak at time= -14, $r = 0.1457$, $n = 276$; $-\log\text{-likelihood} = 3.6539$, $p < 0.05$).

In order to compare the dominant's behaviour to the subordinate's, I must also ask whether the subordinate *approached* the dominant. At the moment that the chimpanzees were in different quadrants, the subordinate did not *approach*, but she did walk towards the dominant significantly more than expected several seconds later.

Cross Correlation, Pair 2 Competition: When Both Chimpanzees are in Different Quadrants, Does the Subordinate Walk Towards the Dominant?

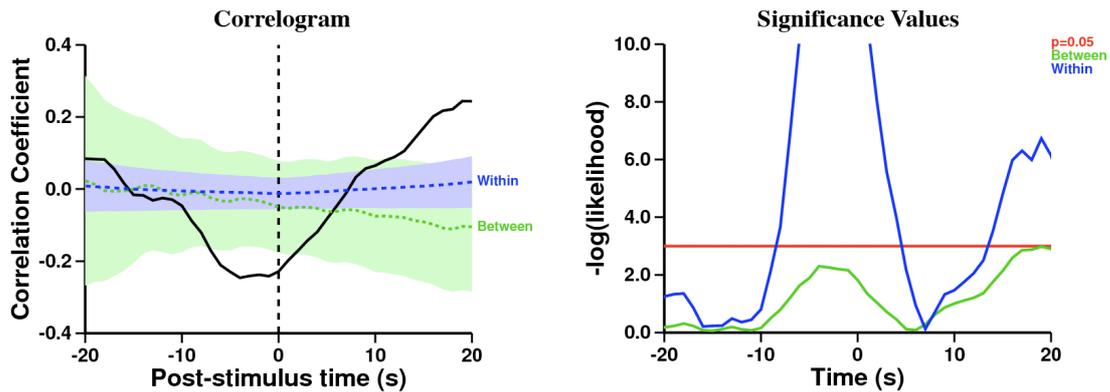


FIGURE 5.50: Referent behaviour: both chimpanzees are in different quadrants. Target behaviour: subordinate walking towards the dominant. Before, and including the moment that the chimpanzees were in different quadrants, the subordinate walked towards the dominant significantly less than expected from the within-trial shuffled control (peak at time= -1, $r = -0.2417$, $n = 433$; $-\log\text{-likelihood} = 15.0350$, $p < 0.05$). After the chimpanzees were in different quadrants, the subordinate walked towards the dominant significantly more than expected (peak at time= +19, $r = 0.2439$, $n = 137$; $-\log\text{-likelihood} = 6.7299$, $p < 0.05$).

However, *approach* behaviour was not consistent throughout the 24 trials of the experiment. Therefore, I divided the analysis into three distinct phases, based on changes in either subject's behaviour.

2. Phase 1

Approach behaviour was markedly different between the phases, but in general very similar between subjects. During Phase 1, at the moment that the chimpanzees were in different quadrants, the dominant was unlikely to be walking towards the subordinate, but when the subordinate had taken several steps into a different quadrant, the dominant did *approach* her (Figure 5.51).

Cross Correlation, Pair 2 Phase 1: When Both Chimpanzees are in Different Quadrants, Does the Dominant Walk Towards the Subordinate?

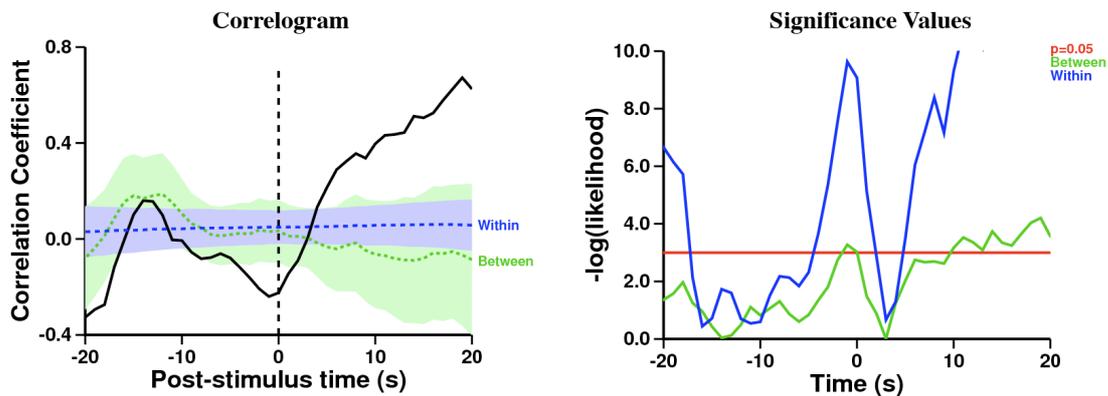


FIGURE 5.51: Referent behaviour: chimpanzees are in different quadrants. Target behaviour: dominant walking towards the subordinate. After the chimpanzees were in different quadrants, the dominant walked towards the subordinate significantly less than expected from the within-trial shuffled control between time = -4 and +1 (peak at time = -1, $r = -0.2401$, $n = 198$; $-\log\text{-likelihood} = 9.6291$, $p < 0.05$). Later, the dominant walked towards the subordinate significantly more than expected from the within-trial shuffled control (peak at time = +19, $r = 0.6724$, $n = 63$; $-\log\text{-likelihood} = 15.4924$, $p < 0.05$).

When the dominant walked towards the subordinate using this type of following, the subordinate was significantly likely to stop walking (Figure 5.52; “Stop” was defined as a change from “Locomotion” to five consecutive seconds of “No Locomotion”).

Cross Correlation, Pair 2 Phase 1: When the Dominant *Approaches* the Subordinate, Does the Subordinate Stop Walking?

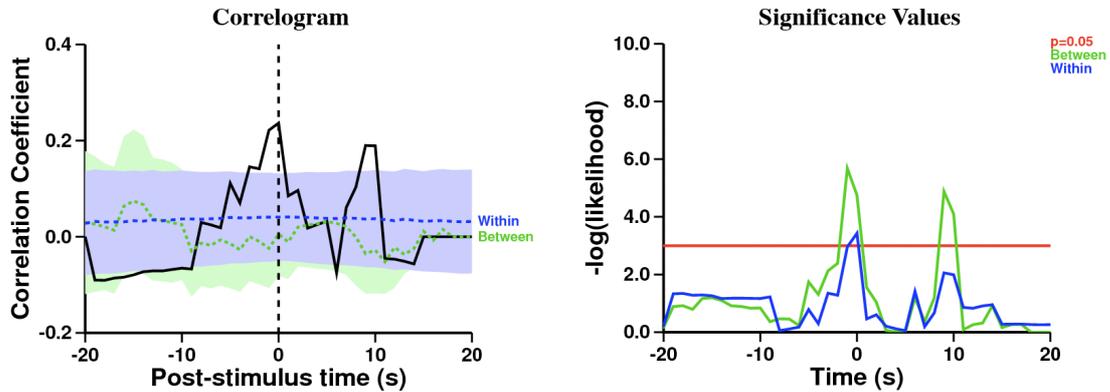


FIGURE 5.52: Referent behaviour: dominant *approaching* the subordinate. Target behaviour: subordinate stops walking for five seconds. At the moment that the dominant *approached* the subordinate, the subordinate stopped walking more than expected from the within-trial shuffled control (peak at time= 0, $r = 0.2364$, $n = 193$; $-\log\text{-likelihood} = 3.4303$, $p < 0.05$).

In Phase 1, the subordinate did not walk towards the dominant when they were together in the same quadrant, and only *approached* the dominant from a different quadrant for a very brief period (Figure 5.53).

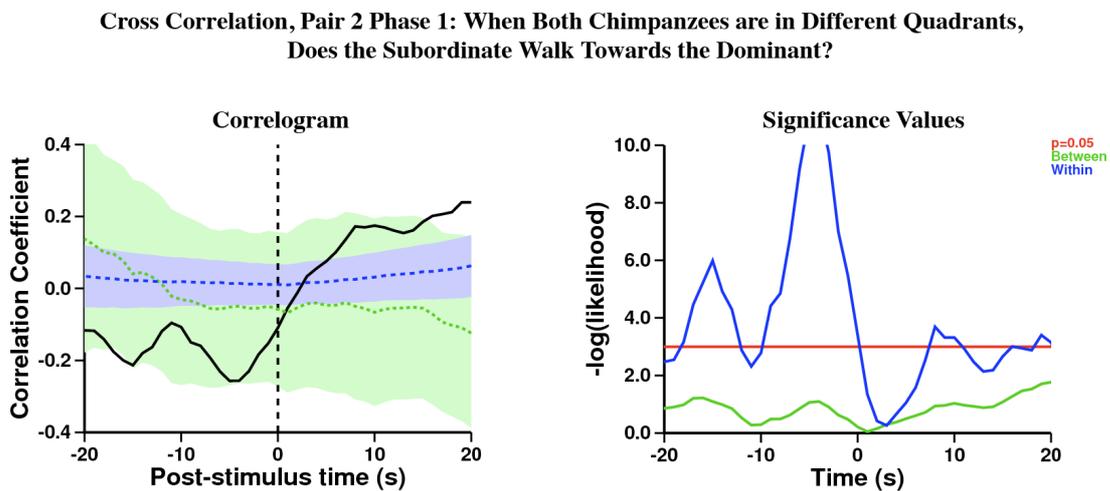


FIGURE 5.53: Referent behaviour: chimpanzees are in different quadrants. Target behaviour: subordinate walking towards the dominant. After the chimpanzees were in different quadrants, the subordinate walked towards the dominant significantly more than expected from the within-trial shuffled control between time= +8 and +10. (Peak at time= +8, $r = 0.1723$, $n = 162$; $-\log\text{-likelihood} = 3.6899$, $p < 0.05$). Furthermore, when the chimpanzees were in the same quadrant before time= 0, the subordinate walked towards the dominant significantly less than expected from the within-trial shuffled control (peak at time= -4, $r = -0.2565$, $n = 194$; $-\log\text{-likelihood} = 11.1970$, $p < 0.05$)

3. Phase 2

In Phase 2, both chimpanzees walked towards their opponent while they were together in the same quadrant, but only the dominant *approached* the subordinate from a different quadrant, with an even greater delay than in Phase 1 (Figures 5.54 and 5.56).

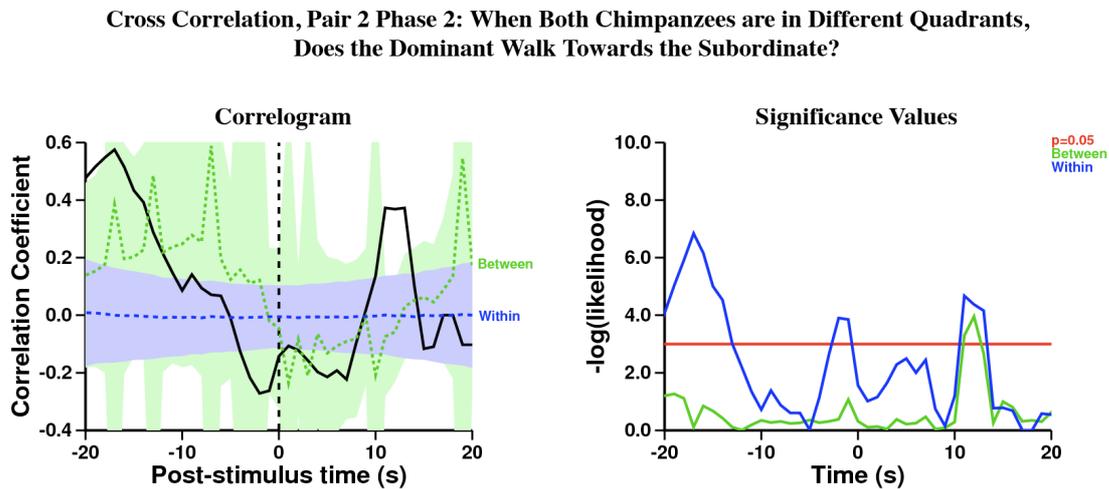


FIGURE 5.54: Referent behaviour: both chimpanzees are in different quadrants. Target behaviour: dominant walks towards the subordinate. After the chimpanzees were in different quadrants, the dominant walked towards the subordinate significantly more than expected from the within trial shuffled control (peak at time= +11, $r = 0.3729$, $n = 44$; $-\log\text{-likelihood} = 4.6734$, $p < 0.05$). Immediately before the chimpanzees were in different quadrants, the dominant did not walk towards the subordinate (peak at time= -2, $r = -0.2715$, $n = 90$; $-\log\text{-likelihood} = 3.9020$, $p < 0.05$), but many seconds before they were in different quadrants, the dominant walked towards the subordinate (peak at time= -17, $r = 0.5752$, $n = 46$; $-\log\text{-likelihood} = 6.8401$, $p < 0.05$), and this could be an artefact of the experimental setup.

Several seconds after the dominant *approached* the subordinate, the subordinate was likely to stop walking, possibly to pause and check that the dominant was a safe distance away before the subordinate ran towards the food (Figure 5.55).

Cross Correlation, Pair 2 Phase 2: When the Dominant *Approaches* the Subordinate, Does the Subordinate Stop Walking?

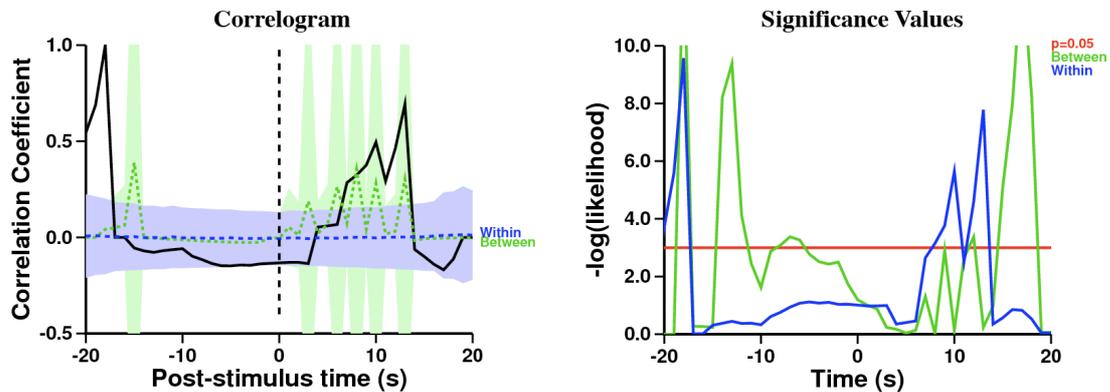


FIGURE 5.55: Referent behaviour: dominant *approaching* the subordinate. Target behaviour: subordinate stops walking. After the dominant walked towards the subordinate from a different quadrant, the subordinate stopped walking more than expected from the within-trial shuffled control (peak at time= +13, $r = 0.6928$, $n = 26$; $-\log\text{-likelihood} = 7.7836$, $p < 0.05$).

On the other hand, during Phase 2 the subordinate walked or ran directly to the location of the hidden food, and therefore did not *approach* the dominant; by the time the chimpanzees were in different quadrants, the subordinate was walking ahead of the dominant to retrieve the banana (Figure 5.56).

Cross Correlation, Pair 2 Phase 2: When Both Chimpanzees are in Different Quadrants,
Does the Subordinate Walk Towards the Dominant?

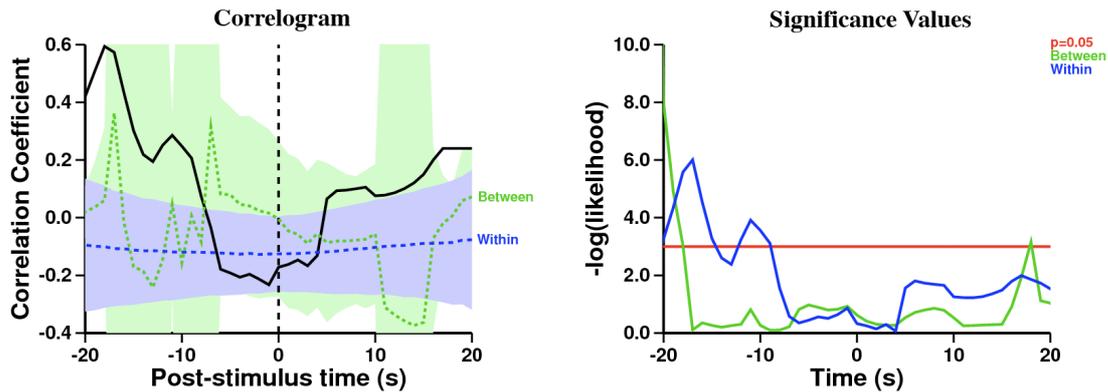


FIGURE 5.56: Referent behaviour: both chimpanzees are in different quadrants. Target behaviour: subordinate walking towards the dominant. Before the chimpanzees were in different quadrants, the subordinate walked towards the dominant significantly more than expected from the within-trial shuffled control (peak at time= -17, $r = 0.5733$, $n = 24$; $-\log\text{-likelihood} = 6.0043$, $p < 0.05$), and this could be an artefact of the experimental setup. After the chimpanzees were in different quadrants, the subordinate walked towards the dominant; this relationship trends towards being more than expected from the within-trial shuffled control (time= +17, $r = 0.2402$, $n = 14$; $-\log\text{-likelihood} = 1.9905$, *ns*).

4. Phase 3

During Phase 3, neither chimpanzee *approached* the other. The dominant did walk towards the subordinate while they were together in the same quadrant, but after they were in different quadrants the dominant walked towards the subordinate significantly less than expected from the within-trial shuffled control (Figure 5.57).

Cross Correlation, Pair 2 Phase 3: When Both Chimpanzees are in Different Quadrants, Does the Dominant Walk Towards the Subordinate?

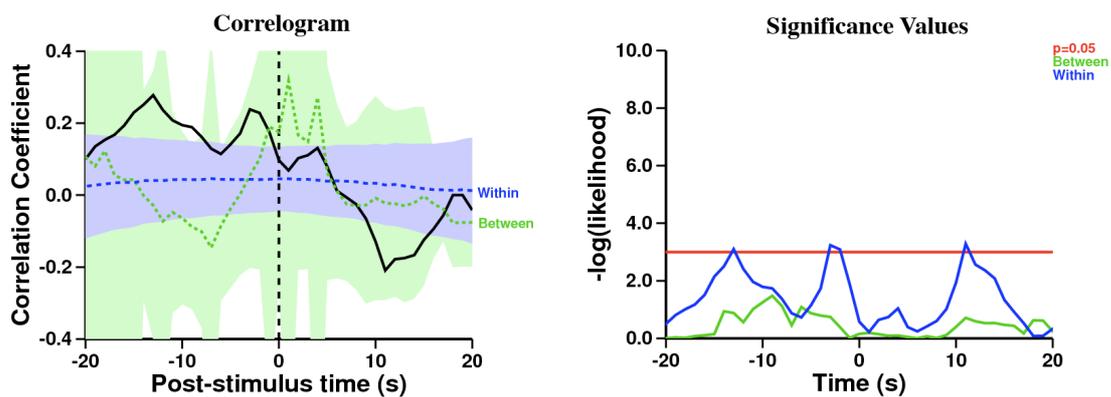


FIGURE 5.57: Referent behaviour: both chimpanzees are in different quadrants. Target behaviour: dominant walking towards the subordinate. After the chimpanzees were in different quadrants, the dominant walked towards the subordinate significantly less than expected from the within-trial shuffled control for one second (peak at time= +11, $r = -0.2093$, $n = 66$; $-\log\text{-likelihood} = 3.2875$, $p < 0.05$). Before they were in different quadrants, the dominant walked towards the subordinate (peak at time= -3, $r = 0.2383$, $n = 128$; $-\log\text{-likelihood} = 3.2361$, $p < 0.05$).

Similarly, the subordinate was significantly unlikely to walk towards the dominant both before and after they were in different quadrants (Figure 5.58). The subordinate did briefly walk towards the dominant while they were in the same quadrant, though this may be an artefact of the experimental setup in which the dominant was released into the enclosure before the subordinate.

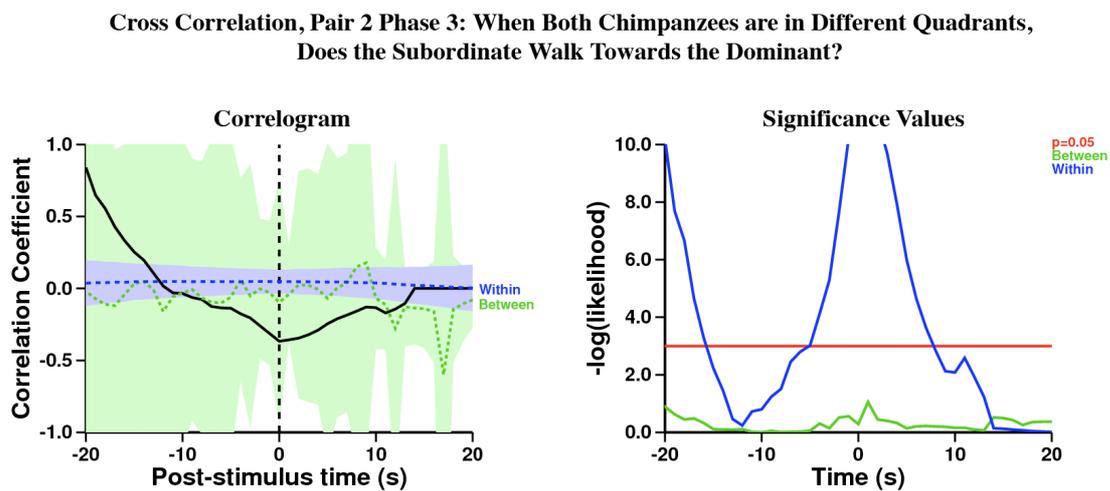


FIGURE 5.58: Referent behaviour: both chimpanzees in different quadrants. Target behaviour: subordinate walking towards the dominant. Both before and after the chimpanzees were in different quadrants, the subordinate was significantly unlikely to be walking towards the dominant (peak at time= 0, $r = -0.3668$, $n = 142$; $-\log\text{-likelihood} = 13.4635$, $p < 0.05$). Before the chimpanzees were in different quadrants, the subordinate walked towards the dominant and this could be an artefact of the experimental setup (peak at time= -20, $r = 0.8402$, $n = 25$; $-\log\text{-likelihood} = 10.1787$, $p < 0.05$).

The overall dataset showed that both subjects *approached* their opponent, but the phase-by-phase analysis has been valuable in that it has shown that this pattern is inconsistent throughout each phase of the experiment. At the beginning, the dominant was eager to search the enclosure for the banana, and *approached* the subordinate through Phases 1 and 2, but during Phase 2 when the dominant *approached*, the subordinate paused her movement. By the third phase, the dominant had abandoned her *approach* tactic. While the subordinate walked towards the dominant from a different quadrant in Phase 1, in Phase 2 as soon as the dominant entered another quadrant, the subordinate stopped walking, and in Phase 3 the subordinate did not *approach* the dominant.

5. *No Knowledge* controls

During the control trials, the *approach* behaviour was very different between the two subjects. In the *No Knowledge* controls, the dominant did not walk towards the subordinate while they were in the same quadrant, but did *approach* the subordinate when they were in different quadrants (Figure 5.59). The dominant was very motivated to search during the *No Knowledge* controls and continued to *approach* the subordinate, possibly because she had learned over the course of 20 competitive trials that this was sometimes an effective tactic to gain information from her about the food's location, or perhaps she wanted to stay close to the subordinate to maintain social cohesion.

**Cross Correlation, Pair 2 *No Knowledge*: When Both Chimpanzees are in Different Quadrants,
Does the Dominant Walk Towards the Subordinate?**

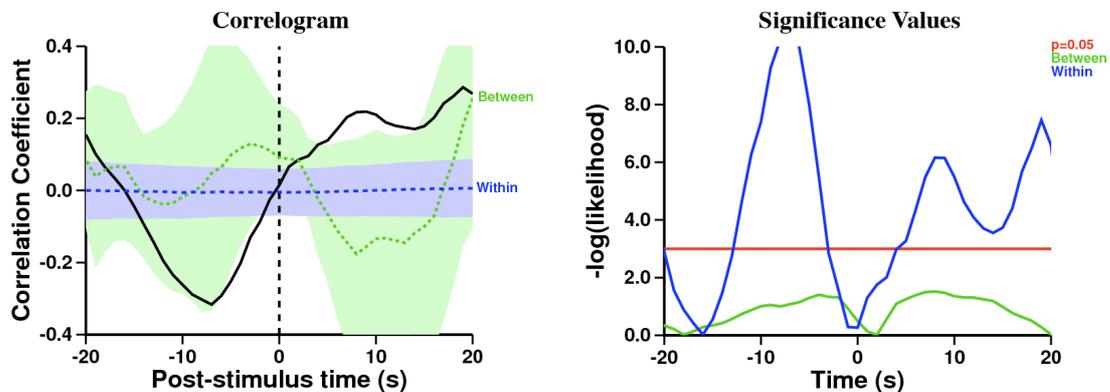


FIGURE 5.59: Referent behaviour: both chimpanzees in different quadrants. Target behaviour: dominant walking towards the subordinate. Before the chimpanzees were in different quadrants, the dominant walked towards the subordinate significantly less than expected from the within-trial shuffled control (peak at time= -7, $r = -0.3166$, $n = 182$; $-\log\text{-likelihood} = 11.3750$, $p < 0.05$). After the chimpanzees were in different quadrants, the dominant walked towards the subordinate significantly more than expected (peak at time= +19, $r = 0.2861$, $n = 143$; $-\log\text{-likelihood} = 7.4612$, $p < 0.05$).

The subordinate had the opposite *approach* pattern: she was significantly unlikely to *approach* the dominant until they were in different quadrants for many seconds (Figure 5.60).

Cross Correlation, Pair 2 No Knowledge: When Both Chimpanzees are in Different Quadrants, Does the Subordinate Walk Towards the Dominant?

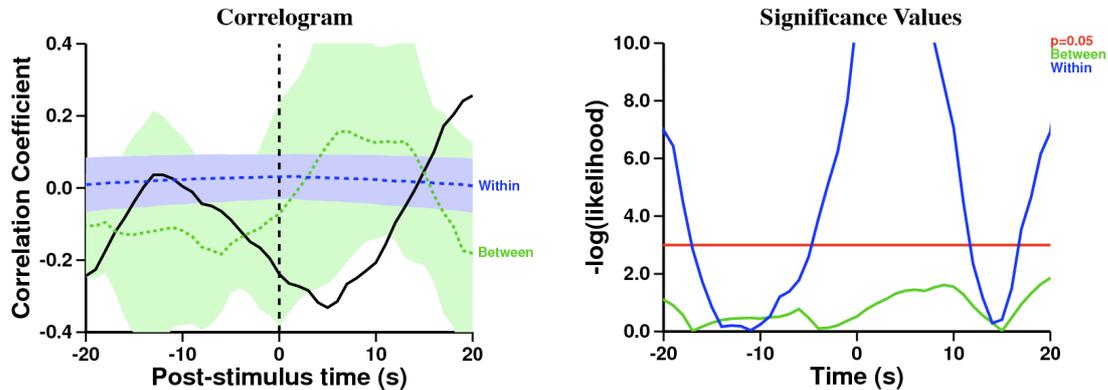


FIGURE 5.60: Referent behaviour: both chimpanzees in different quadrants. Target behaviour: subordinate walking towards the dominant. Both before and after the chimpanzees were in different quadrants, the subordinate walked towards the dominant significantly less than expected from the within-trial shuffled control (peak at time= +5, $r = -0.3319$, $n = 235$; $-\log\text{-likelihood} = 16.4729$, $p < 0.05$). Many seconds after the chimpanzees were in different quadrants, the subordinate walked towards the dominant significantly more than expected (peak at time= +20, $r = 0.2563$, $n = 157$; $-\log\text{-likelihood} = 6.9196$, $p < 0.05$). Before the chimpanzees were in different quadrants, the subordinate did not walk towards the dominant (peak at time= -20, $r = -0.2437$, $n = 159$; $-\log\text{-likelihood} = 6.9852$, $p < 0.05$).

6. Full Knowledge controls

During the *Full Knowledge* controls, there was insufficient data to show either chimpanzee *approaching* the other from different quadrants (and therefore no Figures). The dominant ran ahead of the subordinate towards the reward, and the subordinate did not walk towards her—either she walked away, sat down, or did not enter the enclosure.

7. No Bait, No Knowledge controls

During the *No Bait, No Knowledge* controls, the dominant did not walk towards the subordinate, either before or after they were in different quadrants (Figure 5.61); in contrast, the subordinate did *approach* the dominant after spending some time in a different quadrant (Figure 5.62).

Cross Correlation, Pair 2 No Bait, No Knowledge: When Both Chimpanzees are in Different Quadrants, Does the Dominant Walk Towards the Subordinate?

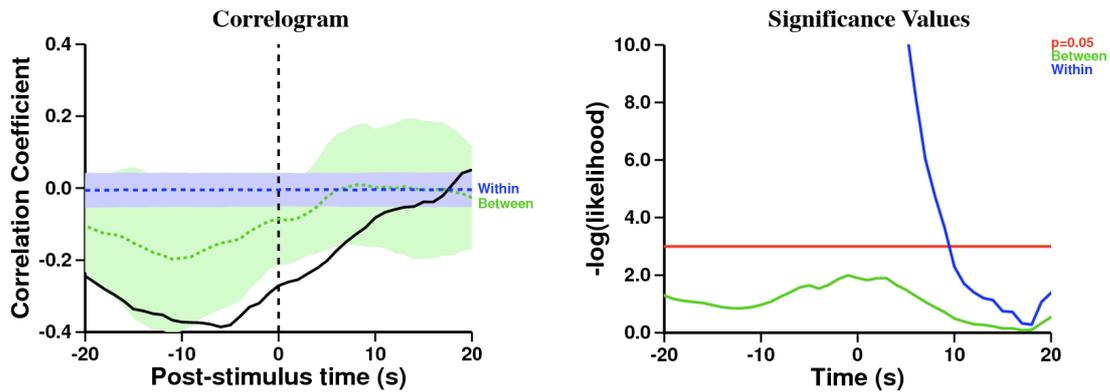


FIGURE 5.61: Referent behaviour: both chimpanzees are in different quadrants. Target behaviour: dominant walking towards the subordinate. Both before and after the chimpanzees were in different quadrants, the dominant walked towards the subordinate significantly less than expected from the within-trial shuffled control (peak at time = -5, $r = -0.3808$, $n = 491$; $-\log(\text{likelihood}) = 32.4387$, $p < 0.05$).

Cross Correlation, Pair 2 No Bait, No Knowledge: When Both Chimpanzees are in Different Quadrants, Does the Subordinate Walk Towards the Dominant?

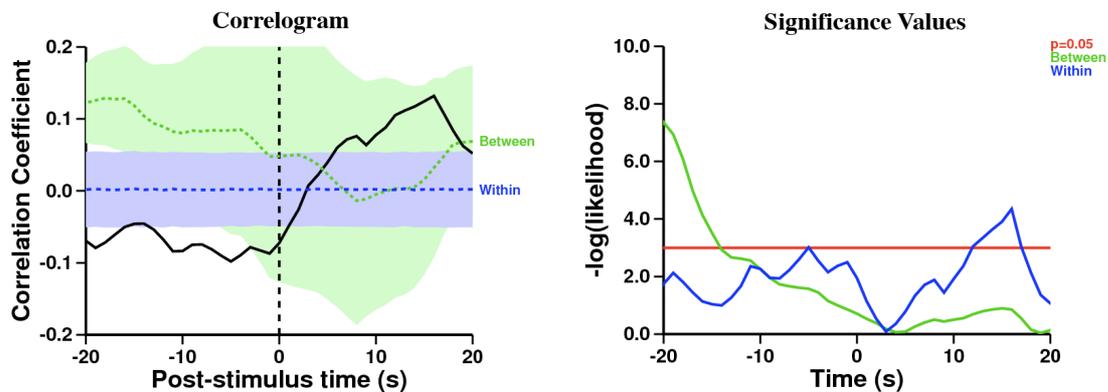


FIGURE 5.62: Referent behaviour: both chimpanzees are in different quadrants. Target behaviour: subordinate walking towards the dominant. After the chimpanzees were in different quadrants, the subordinate walked towards the dominant significantly more than expected from the within-trial shuffled control between time= +12 and +17 (peak at time= +16, $r = 0.1319$, $n = 398$; $-\log\text{-likelihood} = 4.3485$, $p < 0.05$). Before they were in different quadrants (before time= 0), the relationship was significantly less than expected from the within-trial shuffled control for one second (time= -5, $r = -0.0981$, $n = 447$; $-\log\text{-likelihood} = 3.0126$, $p < 0.05$).

8. Summary of *Approach* behaviour

Approach behaviour was found to be different between the three phases of the *Competition*, but within each phase each subject *approached* the other in a similar manner. Differences between the chimpanzees' *approach* behaviour were found in the *No Knowledge* and *No Bait, No Knowledge* controls. In the overall *Competition* dataset, each subject only *approached* her opponent significantly more than expected after spending many seconds in different quadrants. During Phase 1, both subjects *approached* their opponent. In Phase 2, both chimpanzees walked towards their competitor while they were in the same quadrant, but only the dominant *approached* the subordinate from a different quadrant. Though the subordinate ran to the food on many trials in this phase, on a few, the dominant *approached* the subordinate, causing the subordinate to stop walking; as soon as the subordinate stopped, the dominant overtook her, and the subordinate did not *approach* the dominant. In Phase 3, neither chimpanzee *approached* the other. During the *No Knowledge* control trials, the dominant did not walk towards the subordinate while they were in the same quadrant, though the subordinate did walk towards the dominant. After they were in different quadrants, the

dominant did *approach* the subordinate, but the subordinate did not *approach* the dominant until much later. There was no evidence of *approach* behaviour from the *Full Knowledge* controls. In the *No Bait, No Knowledge* controls, the dominant did not *approach*, and the subordinate did *approach* the dominant after spending many seconds in different quadrants.

G. Footsteps

I will describe the patterns of walking in the other's *footsteps* in the same manner for the entire dataset, for each of the three distinct phases, and then for the three controls.

Footsteps was defined as “both subjects are in the same quadrant and both are walking towards the same (any) quadrant, and one individual is walking towards the other and the other walking away from the first individual.”

1. Entire Competition dataset

The chimpanzees walked towards each other while in the same quadrant, and so I addressed whether either chimpanzee followed in the *footsteps* of the other. It seemed that within this pair, the dominant had more success in exploiting the subordinate by staying close to her; when the dominant paused or searched elsewhere, the subordinate would often take the opportunity to run ahead to where the food was hidden. The dominant walked in the subordinate's *footsteps* significantly more than expected from the within-trial shuffled control (Figure 5.63).

Cross Correlation, Pair 2 Competition: When Both Chimpanzees are in the Same Quadrant and Walking Towards the Same Quadrant, Does the Dominant Walk Towards the Subordinate, and the Subordinate Walk Away From the Dominant?

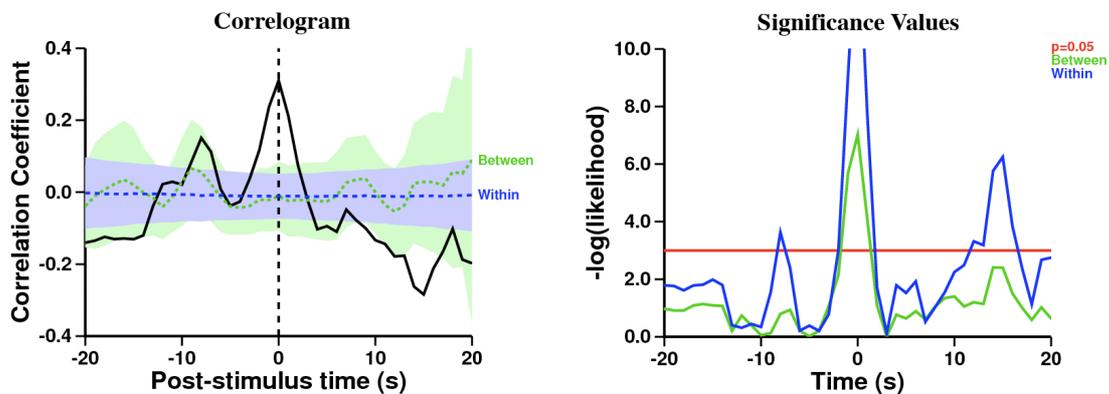


FIGURE 5.63: Referent behaviour: chimpanzees are both in the same quadrant and both walking towards the same quadrant. Target behaviour: dominant walking towards the subordinate and the subordinate walking away from the dominant. At the moment that the chimpanzees were in the same quadrant and walking towards the same quadrant, the dominant walked towards the subordinate and the subordinate walked away from the dominant significantly more than expected from the within-trial shuffled control (peak at time= 0, $r = 0.3106$, $n = 324$; $-\log\text{-likelihood} = 14.8105$, $p < 0.05$). Before the chimpanzees were in the same quadrant and walking towards the same quadrant, the dominant walked towards the subordinate, and the subordinate away from the dominant, significantly more than expected (peak at time= -8, $r = 0.1509$, $n = 225$; $-\log\text{-likelihood} = 3.6272$, $p < 0.05$). After the chimpanzees were in the same quadrant for a while, the dominant no longer walked towards the subordinate and the subordinate away from the dominant (peak at time= +15, $r = -0.2843$, $n = 91$; $-\log\text{-likelihood} = 6.2472$, $p < 0.05$).

Conversely, the subordinate did not walk in the dominant's *footsteps* (Figure 5.64). Many seconds before the chimpanzees were in the same quadrant and walking towards the same quadrant, the subordinate did walk towards the dominant, and the dominant away from the subordinate, though this could be an artefact of the experimental setup in which the dominant entered the enclosure before the subordinate. Many seconds after the chimpanzees were in the same quadrant and walking towards the same quadrant, it appeared that the subordinate did follow in the dominant's *footsteps*, however, this result could reflect the dominant's tendency to run ahead of the subordinate.

Cross Correlation, Pair 2 Competition: When Both Chimpanzees are in the Same Quadrant and Walking Towards the Same Quadrant, Does the Subordinate Walk Towards the Dominant, and the Dominant Walk Away From the Subordinate?

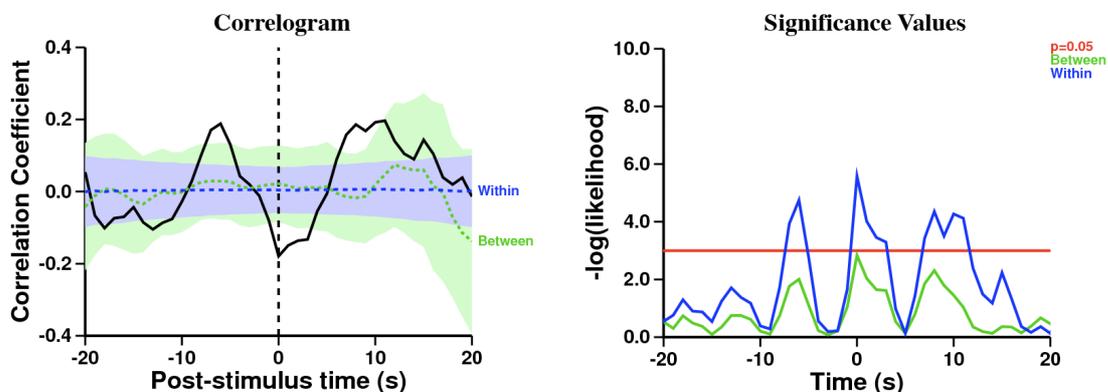


FIGURE 5.64: Referent behaviour: chimpanzees are both in the same quadrant and both walking towards the same quadrant. Target behaviour: subordinate walking towards the dominant and the dominant walking away from the subordinate. At the moment that the chimpanzees were in the same quadrant and walking towards the same quadrant, the subordinate walked towards the dominant and the dominant walked away from the subordinate significantly less than expected from the within-trial shuffled control (peak at time= 0, $r = -0.1794$, $n = 324$; $-\log\text{-likelihood} = 5.5834$, $p < 0.05$). Both before and after this moment at time=0, the relationship is significantly more than expected from the within-trial shuffled control (peak at time=-6, $r = 0.1883$, $n = 256$; $-\log\text{-likelihood} = 4.7499$, $p < 0.05$. peak at time= +8, $r = 0.1859$, $n = 180$; $-\log\text{-likelihood} = 4.3545$, $p < 0.05$).

2. Phase 1

The pattern of following in the other's *footsteps* was different during each phase. During Phase 1 the dominant followed in the subordinate's *footsteps* (Figure 5.65), whereas the subordinate initially did not follow in the dominant's *footsteps* but then did follow the dominant significantly more than expected from the within-trial shuffled control (Figure 5.66).

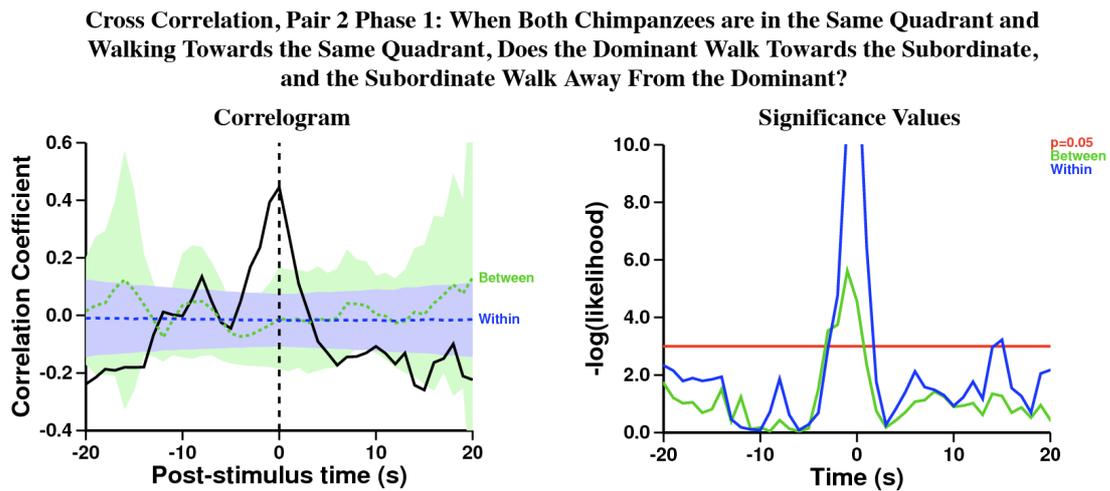


FIGURE 5.65: Referent behaviour: chimpanzees are both in the same quadrant and both walking towards the same quadrant. Target behaviour: dominant walking towards the subordinate and the subordinate walking away from the dominant. At the moment that the chimpanzees were in the same quadrant and walking towards the same quadrant, the dominant walked towards the subordinate and the subordinate walked away from the dominant significantly more than expected from the within-trial shuffled control (peak at time= 0, $r = 0.4453$, $n = 160$; $-\log\text{-likelihood} = 13.7550$, $p < 0.05$). Many seconds later, the dominant walked towards the subordinate and the subordinate away from the dominant significantly less than expected for one second (time= +15, $r = -0.2593$, $n = 63$; $-\log\text{-likelihood} = 3.2235$, $p < 0.05$).

Cross Correlation, Pair 2 Phase 1: When Both Chimpanzees are in the Same Quadrant and Walking Towards the Same Quadrant, Does the Subordinate Walk Towards the Dominant, and the Dominant Walk Away From the Subordinate?

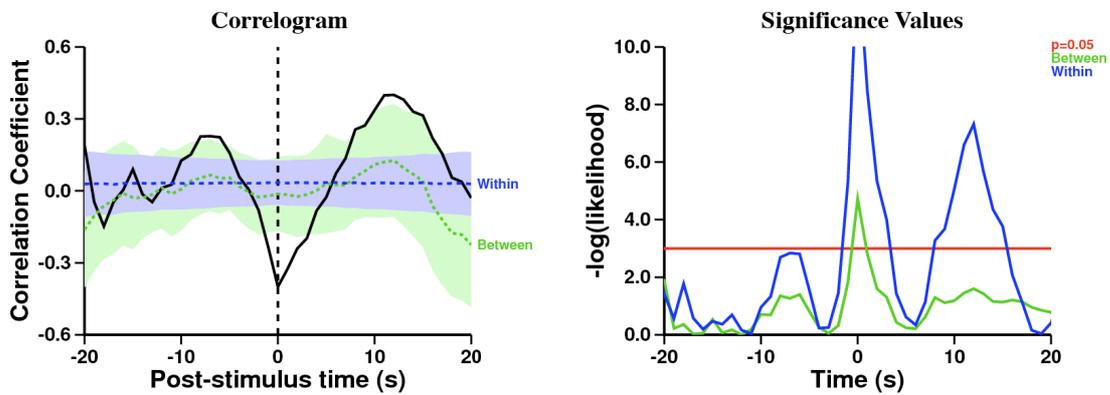


FIGURE 5.66: Referent behaviour: chimpanzees are both in the same quadrant and both walking towards the same quadrant. Target behaviour: subordinate walking towards the dominant and the dominant walking away from the subordinate. At the moment that the chimpanzees were in the same quadrant and walking towards the same quadrant, the subordinate walked towards the dominant and the dominant walked away from the subordinate significantly less than expected from the within-trial shuffled control (peak at time= 0, $r = -0.4235$, $n = 160$; $-\log\text{-likelihood} = 13.2490$, $p < 0.05$). Many seconds later, the relationship became significantly more than expected from the within-trial shuffled control (peak at time= +12, $r = 0.4300$, $n = 72$; $-\log\text{-likelihood} = 7.3190$, $p < 0.05$).

The pattern in the graphs indicates that the subordinate initially did not follow the dominant, but that twelve seconds later it appeared that she did; this is a good example of a graphical depiction of the interaction between the two chimpanzees in which the dominant ran ahead of the subordinate—giving the appearance that the subordinate was following in the *footsteps* of the dominant.

3. Phase 2

Though *footsteps* behaviour is not significant in Phase 2, it is worthwhile to consider the pattern in the data: whether the correlation coefficients increase or decrease. During Phase 2, the dominant did walk in the subordinate's footsteps briefly, then the pattern fluctuates but with an overall downward trend, such that many seconds after the two chimpanzees are in the same quadrant and walking towards the same quadrant, the dominant did not walk in the subordinate's *footsteps* (Figure 5.67).

Cross Correlation, Pair 2 Phase 2: When Both Chimpanzees are in the Same Quadrant and Walking Towards the Same Quadrant, Does the Dominant Walk Towards the Subordinate, and the Subordinate Walk Away From the Dominant?

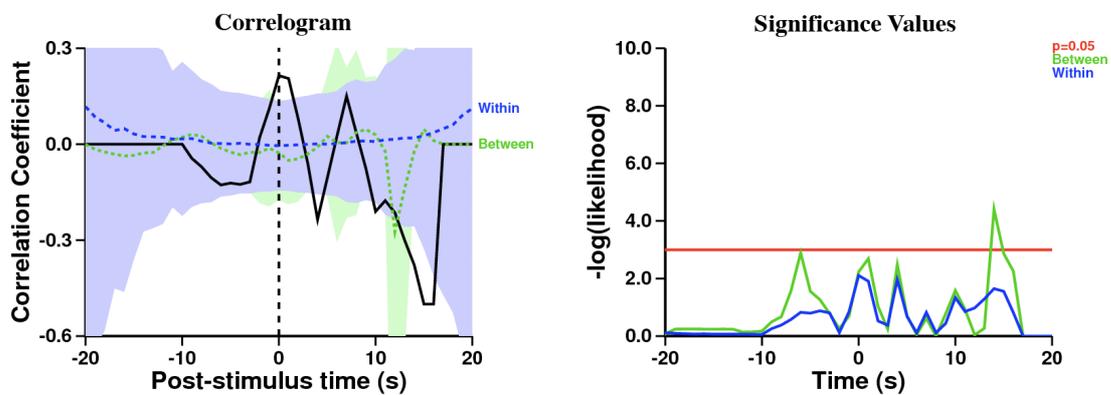


FIGURE 5.67: Referent behaviour: chimpanzees are both in the same quadrant and both walking towards the same quadrant. Target behaviour: dominant walking towards the subordinate and the subordinate walking away from the dominant. After the chimpanzees were in the same quadrant and walking towards the same quadrant, the dominant walked towards the subordinate and the subordinate walked away from the dominant; this relationship trends towards being more than expected from the within-trial shuffled control (peak at time= 0, $r = 0.2144$, $n = 63$; $-\log\text{-likelihood} = 2.1038$, ns). Then, the dominant did not walk towards the subordinate and the subordinate away from the dominant; this relationship trends towards being less than expected from the within-trial shuffled control (peak at time= +4, $r = -0.2359$, $n = 44$; $-\log\text{-likelihood} = 1.9618$, ns).

The correlogram of the subordinate's behaviour exhibits a similar fluctuation, showing that at the moment that the chimpanzees were in the same quadrant and walking towards the same quadrant, the subordinate did not follow in the dominant's *footsteps* (Figure 5.68); but both a few seconds before and a few seconds after the chimpanzees were in the same quadrant and walking towards the same quadrant, the subordinate walked towards the dominant, and the dominant walked away from the subordinate.

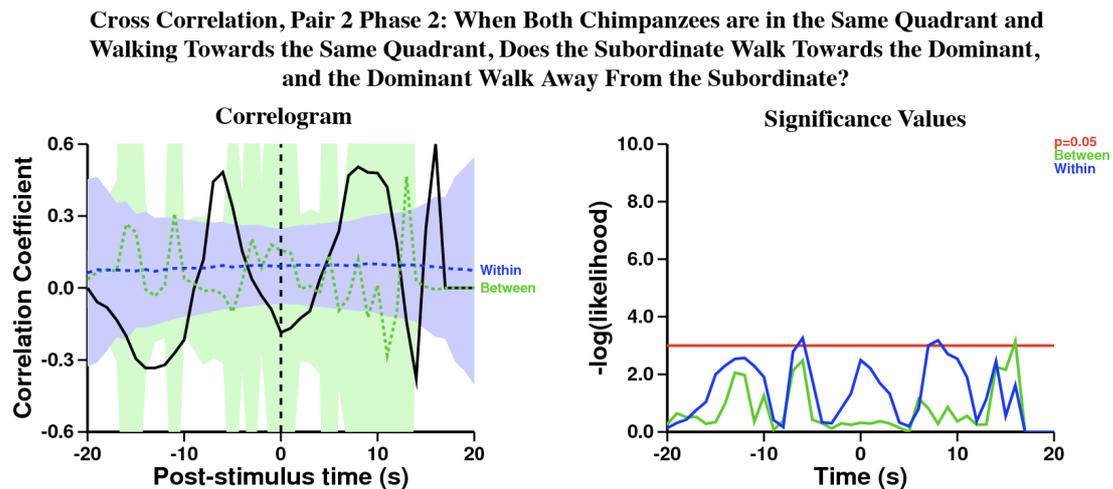


FIGURE 5.68: Referent behaviour: chimpanzees are both in the same quadrant and both walking towards the same quadrant. Target behaviour: subordinate walking towards the dominant and the dominant walking away from the subordinate. After the chimpanzees were in the same quadrant and walking towards the same quadrant, the subordinate did not walk towards the dominant and the dominant did not walk away from the subordinate; this relationship trends towards being less than expected from the within-trial shuffled control (peak at time= 0, $r = -0.1857$, $n = 63$; $-\log\text{-likelihood} = 2.4915$, ns). Both before and after the chimpanzees were in the same quadrant and walking towards the same quadrant, the subordinate walked towards the dominant and the dominant walked away from the subordinate (peak at time= -6, $r = 0.4828$, $n = 47$; $-\log\text{-likelihood} = 3.2612$, $p < 0.05$. peak at time= +8, $r = 0.5048$, $n = 30$; $-\log\text{-likelihood} = 3.1794$, $p < 0.05$).

The opposite pattern of fluctuation between both chimpanzees shows the dynamic nature of their following: that the dominant follows the subordinate, runs ahead to search, the subordinate passes her, and the dominant is once again following in the subordinate's *footsteps*. These correlograms successfully capture the “continuous feedback” between the chimpanzees' movement.

4. Phase 3

In Phase 3, the chimpanzees' behaviour was different from the previous two phases. The dominant walked towards the subordinate and the subordinate walked away from the dominant before they were in the same quadrant and walking towards the same quadrant, but overall the dominant did not walk in the subordinate's *footsteps* significantly more than expected from the within-trial shuffled control (Figure 5.69).

Cross Correlation, Pair 2 Phase 3: When Both Chimpanzees are in the Same Quadrant and Walking Towards the Same Quadrant, Does the Dominant Walk Towards the Subordinate, and the Subordinate Walk Away From the Dominant?

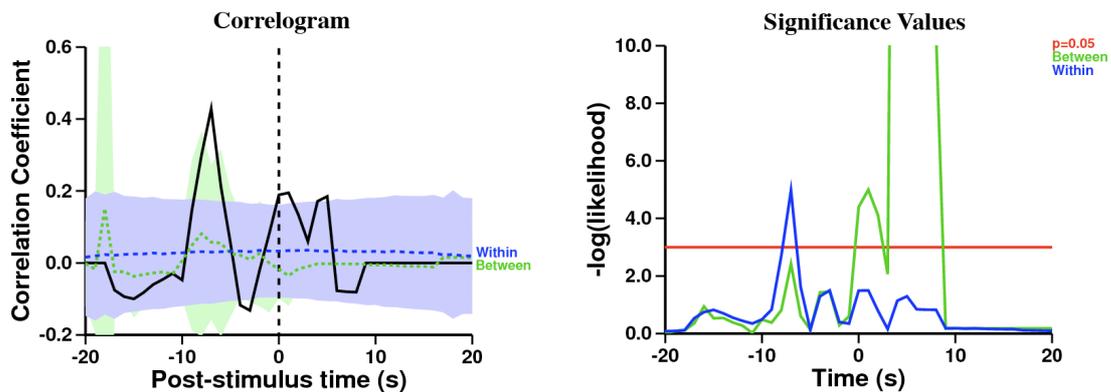


FIGURE 5.69: Referent behaviour: chimpanzees are both in the same quadrant and both walking towards the same quadrant. Target behaviour: dominant walking towards the subordinate and the subordinate walking away from the dominant. Before the chimpanzees were in the same quadrant and walking towards the same quadrant, the dominant walked towards the subordinate and the subordinate walked away from the dominant (peak at time = -7, $r = 0.4286$, $n = 80$; $-\log\text{-likelihood} = 4.9756$, $p < 0.05$).

Additionally, the subordinate walked in the dominant's *footsteps*, opposite from the previous two phases (Figure 5.70).

Cross Correlation, Pair 2 Phase 3: When Both Chimpanzees are in the Same Quadrant and Walking Towards the Same Quadrant, Does the Subordinate Walk Towards the Dominant, and the Dominant Walk Away From the Subordinate?

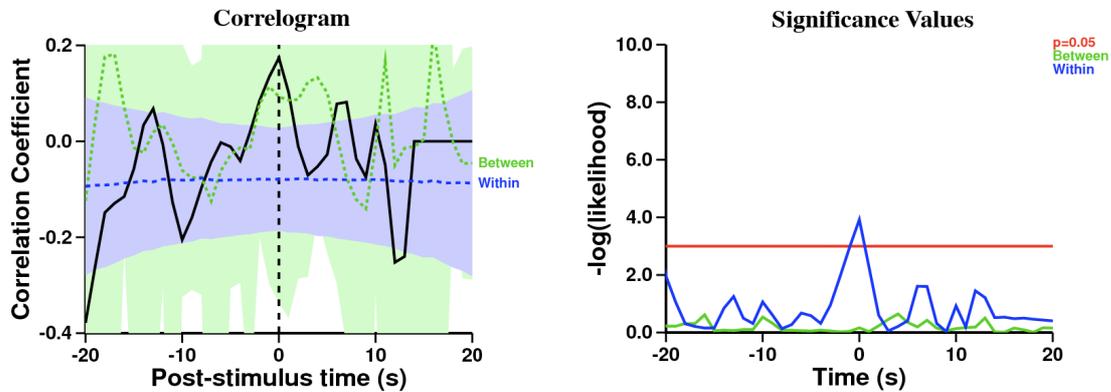


FIGURE 5.70: Referent behaviour: chimpanzees are both in the same quadrant and both walking towards the same quadrant. Target behaviour: subordinate walking towards the dominant and the dominant walking away from the subordinate. At the moment that the chimpanzees were together in the same quadrant and walking towards the same quadrant, the subordinate walked towards the dominant, and the dominant walked away from the subordinate, (peak at time= 0, $r = 0.1740$, $n = 101$; $-\log\text{-likelihood} = 3.9221$, $p < 0.05$).

The three-phase analysis has again shown that both subjects' behaviour changed considerably over time: both subjects' behaviour in Phase 1 became the opposite by Phase 3. In Phase 1, the dominant followed in the subordinate's *footsteps* whereas the subordinate did not follow in the dominant's *footsteps*. In Phase 2, both subjects' behaviour alternated and the correlograms demonstrated that the chimpanzees took turns following in each other's *footsteps*. In Phase 3, the subordinate followed the dominant, but the dominant no longer followed in the subordinate's *footsteps*.

5. No Knowledge controls

In the *No Knowledge* controls, neither subject followed in the other's *footsteps*, and in fact the dominant significantly avoided following the subordinate (Figure 5.71). The subordinate walked toward the dominant before they were together in the same quadrant, which may be an artefact of the experimental setup (Figure 5.72). After they were in the same quadrant and walking towards the same quadrant, there is a trend of the subordinate following in the dominant's *footsteps*, but this relationship was not significant.

Cross Correlation, Pair 2 No Knowledge: When Both Chimpanzees are in the Same Quadrant and Walking Towards the Same Quadrant, Does the Dominant Walk Towards the Subordinate, and the Subordinate Walk Away From the Dominant?

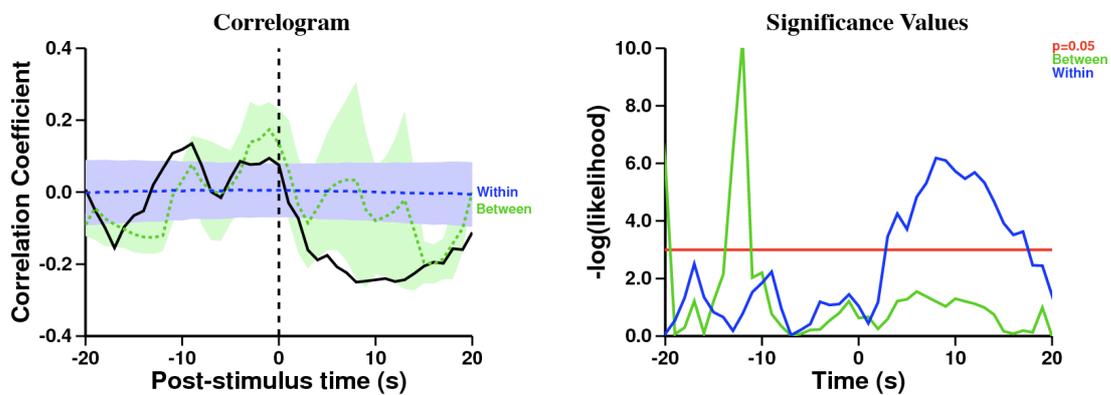


FIGURE 5.71: Referent behaviour: chimpanzees are both in the same quadrant and both walking towards the same quadrant. Target behaviour: dominant walking towards the subordinate and the subordinate walking away from the dominant. After the chimpanzees were in the same quadrant and walking towards the same quadrant, the dominant did not walk towards the subordinate and the subordinate did not walk away from the dominant (peak at time= +8, $r = -0.2502$, $n = 149$; $-\log\text{-likelihood} = 6.1844$, $p < 0.05$).

Cross Correlation, Pair 2 *No Knowledge*: When Both Chimpanzees are in the Same Quadrant and Walking Towards the Same Quadrant, Does the Subordinate Walk Towards the Dominant, and the Dominant Walk Away From the Subordinate?

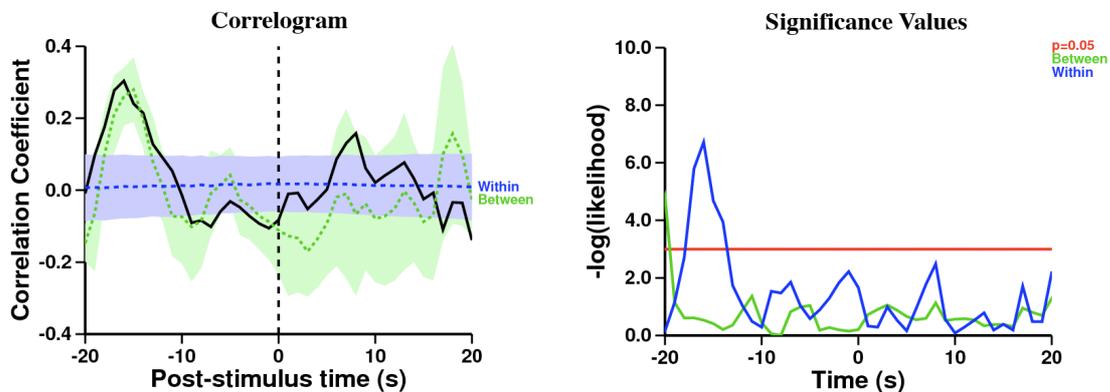


FIGURE 5.72: Referent behaviour: chimpanzees are both in the same quadrant and both walking towards the same quadrant. Target behaviour: subordinate walking towards the dominant and the dominant walking away from the subordinate. Many seconds before the chimpanzees were in the same quadrant and walking towards the same quadrant, the subordinate walked towards the dominant and the dominant away from the subordinate significantly more than expected from the within-trial shuffled control (peak at time= -16, $r=0.3038$, $n=122$; $-\log\text{-likelihood}=6.7160$, $p<0.05$). After the chimpanzees were together in the same quadrant and walking towards the same quadrant, the relationship trends towards being more than expected from the within-trial shuffled control (time= +8, $r=0.1580$, $n=149$; $-\log\text{-likelihood}=2.4864$, *ns*).

6. Full Knowledge controls

During the *Full Knowledge* controls, there was insufficient data to show either chimpanzee following in the *footsteps* of the other (and therefore no figures). When the dominant knew where the food was hidden, she ran to retrieve it, and the subordinate did not follow.

7. No Bait, No Knowledge controls

As with the overall *Competition* dataset, during the *No Bait, No Knowledge* control trials, the dominant followed in the subordinate's *footsteps*, but the subordinate did not follow in the *footsteps* of the dominant (Figures 5.73 and 5.74). The timing of the behaviour is slightly longer than in the overall *Competition* dataset, indicating that the dominant followed in the subordinate's *footsteps* for a longer period than during the *Competition*, and the subordinate did not follow the dominant for a longer period.

Cross Correlation, Pair 2 *No Bait, No Knowledge*: When Both Chimpanzees are in the Same Quadrant and Walking Towards the Same Quadrant, Does the Dominant Walk Towards the Subordinate, and the Subordinate Walk Away From the Dominant?

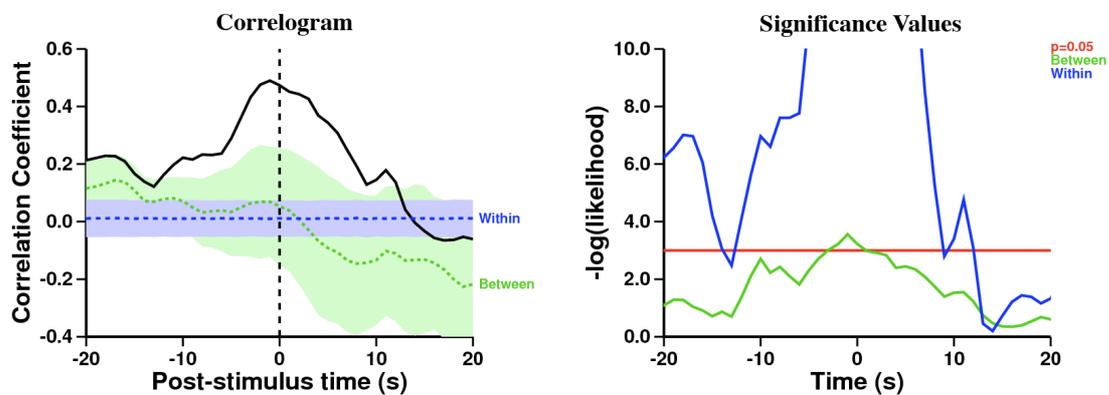


FIGURE 5.73: Referent behaviour: chimpanzees are both in the same quadrant and both walking towards the same quadrant. Target behaviour: dominant walking towards the subordinate and the subordinate walking away from the dominant. Both before and after the chimpanzees were in the same quadrant and walking towards the same quadrant, the dominant walked towards the subordinate and the subordinate walked away from the dominant significantly more than expected (peak at time= -1, $r = 0.4897$, $n = 299$; $-\log\text{-likelihood} = 29.0013$, $p < 0.05$).

Cross Correlation, Pair 2 *No Bait, No Knowledge*: When Both Chimpanzees are in the Same Quadrant and Walking Towards the Same Quadrant, Does the Subordinate Walk Towards the Dominant, and the Dominant Walk Away From the Subordinate?

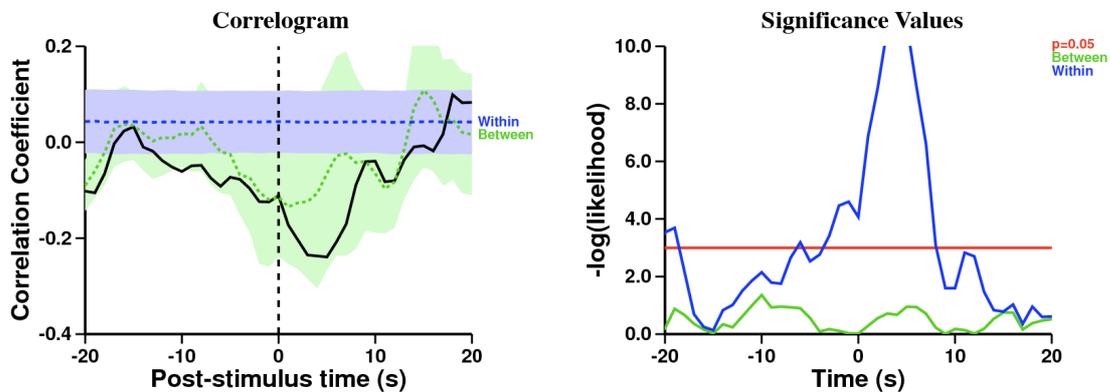


FIGURE 5.74: Referent behaviour: chimpanzees are both in the same quadrant and both walking towards the same quadrant. Target behaviour: subordinate walking towards the dominant and the dominant walking away from the subordinate. After the chimpanzees were in the same quadrant and walking towards the same quadrant, the subordinate did not walk towards the dominant and the dominant did not walk away from the subordinate (peak at time= +5, $r = -0.2393$, $n = 282$; $-\log\text{-likelihood} = 10.7866$, $p < 0.05$).

8. Summary of *Footsteps* behaviour

Where there were differences in knowledge between the two subjects, the dominant was more likely to follow the subordinate than the other way around. Following in the other's *footsteps* varied between phases and between subjects. Both in the overall *Competition* dataset as well as in Phases 1 and 2, the dominant followed in the subordinate's *footsteps*. However, by Phase 3, the dominant no longer followed the subordinate, perhaps due to the subordinate's alternating tactics of walking to the bait and delaying her approach: on the trials in which the subordinate delayed walking to the food reward, following in her *footsteps* would not be a viable strategy for the dominant. In the *No Knowledge* trials, the dominant did not follow in the subordinate's *footsteps*, but during the *No Bait, No Knowledge* trials, she did. On the other hand, the subordinate did not follow in the dominant's footsteps at the overall level or in Phases 1 and 2. In Phase 3, the subordinate did follow in the dominant's *footsteps*. The subordinate did not follow the dominant in either the *No Knowledge* or the *No Bait, No Knowledge* controls. In particular, the chimpanzees' behaviour during Phase 2 seemed to alternate between following and not following, and this could indicate that the dominant initially followed the subordinate, then ran ahead of her, and was then surpassed by the subordinate as she ran ahead to retrieve the food. Hirata and Matsuzawa also reported this

movement type: the ignorant subject “began to run ahead of Chloe’s [informed subject] path” (Hirata & Matsuzawa, 2001, p. 290).

H. *Convergence*

Again I will describe the patterns of *converging* for the entire dataset, for each of the three distinct phases, and then for the three controls. Since *converging* behaviour is conditional on both chimpanzees being in different quadrants, and both walking towards the same quadrant, there is only one graph per condition; it cannot be determined from the correlogram which chimpanzee initiated the movement. However, considering the result that the dominant walked towards three of the four quadrants after the subordinate had started walking in those directions, one can assume that usually the subordinate initiated a movement trajectory and the dominant *converged* her movement to walk towards the same destination.

1. Entire *Competition* dataset

A more sophisticated strategy than following in her competitor’s footsteps would be for the dominant to notice the direction of movement of the subordinate, *converge* on her destination, and then walk towards that destination, though it may be from a different starting point or in a different absolute direction from the subordinate. The correlogram in Figure 5.75 indicates that when the two chimpanzees were in different quadrants, they walked towards the same quadrant.

**Cross Correlation, Pair 2 Competition: When Both Chimpanzees are in Different Quadrants,
Do They Both Walk Towards the Same Quadrant?**

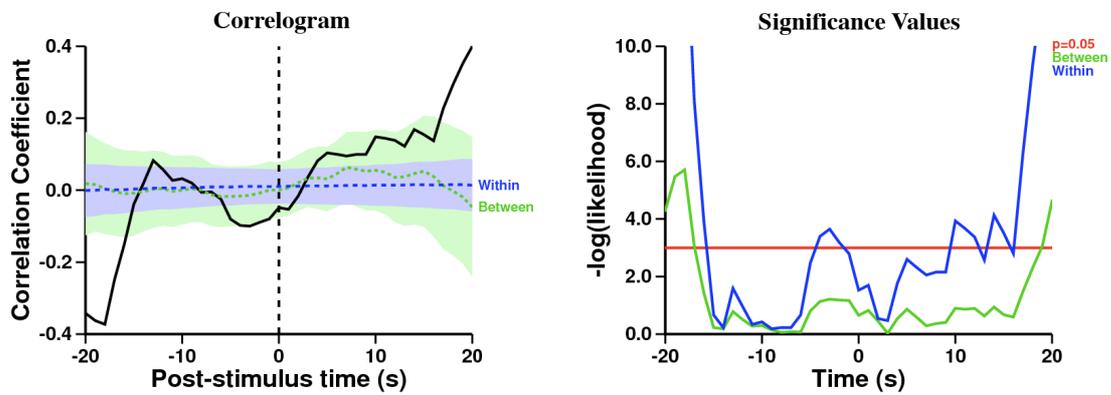


FIGURE 5.75: Referent behaviour: both chimpanzees are in different quadrants. Target behaviour: both chimpanzees walking towards the same quadrant. Before both chimpanzees were in the same quadrant, they were not walking towards the same quadrant (peak at time= -18, $r = -0.3729$, $n = 150$; $-\log\text{-likelihood} = 15.3831$, $p < 0.05$). Peak at time= -4, $r = -0.0981$, $n = 458$; $-\log\text{-likelihood} = 3.3954$, $p < 0.05$). After both chimpanzees were in the same quadrant, they walked towards the same quadrant (peak at time= +20, $r = 0.4616$, $n = 123$; $-\log\text{-likelihood} = 18.3600$, $p < 0.05$).

2. Phase 1

The data are different in each phase. In Phase 1, when the chimpanzees were in the same quadrant they did not walk towards the same quadrant, but after they were in different quadrants they did *converge* and walk towards the same quadrant (Figure 5.76).

Cross Correlation, Pair 2 Phase 1: When Both Chimpanzees are in Different Quadrants, Do They Both Walk Towards the Same Quadrant?

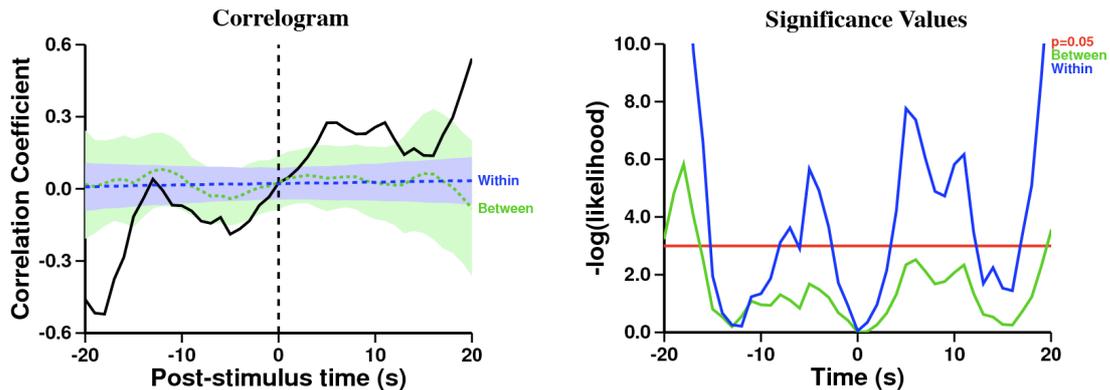


FIGURE 5.76: Referent behaviour: both chimpanzees are in different quadrants. Target behaviour: both chimpanzees walking towards the same quadrant. After both chimpanzees were in the same quadrant, they both walked towards the same quadrant (peak at time= +5, $r = 0.2746$, $n = 214$; $-\log\text{-likelihood} = 7.7604$, $p < 0.05$). Many seconds after they were in the same quadrant, both chimpanzees walked towards the same quadrant significantly more than expected from the within-trial shuffled control (peak at time= +20, $r = 0.5418$, $n = 73$; $-\log\text{-likelihood} = 13.1421$, $p < 0.05$). Before they were in different quadrants (before time= 0), the chimpanzees did not walk towards the same quadrant (peak at time= -5, $r = -0.1889$, $n = 214$; $-\log\text{-likelihood} = 5.6643$, $p < 0.05$). Long before they were in different quadrants, both chimpanzees walked towards the same quadrant significantly less than expected from the within-trial shuffled control (peak at time = -18, $r = -0.5213$, $n = 87$; $-\log\text{-likelihood} = 15.7548$, $p < 0.05$).

However, both subjects paused while *converging* (Figures 5.77 and 5.78). It is likely that during these times each competitor was actively monitoring the movement of the other—a hypothesis that will be explored in the next chapter on Gaze Following.

**Cross Correlation, Pair 2 Phase 1: When Both Chimpanzees *Extrapolate*,
Does the Dominant Stop Walking?**

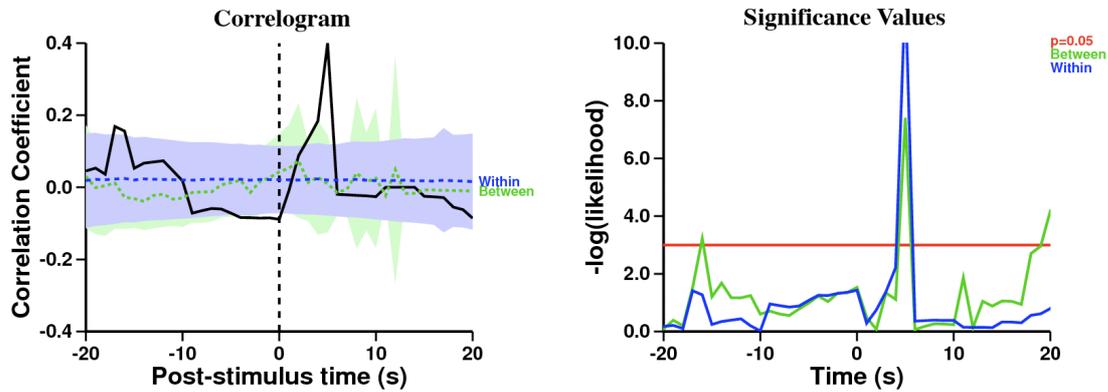


FIGURE 5.77: Referent behaviour: both chimpanzees *converging*. Target behaviour: dominant stops walking for five seconds. After the chimpanzees were in different quadrants and walking towards the same quadrant, the dominant stopped walking significantly more than expected from the within-trial shuffled control (peak at time= +5, $r = 0.4832$, $n = 126$; $-\log\text{-likelihood} = 11.9046$, $p < 0.05$).

**Cross Correlation, Pair 2 Phase 1: When Both Chimpanzees *Extrapolate*,
Does the Subordinate Stop Walking?**

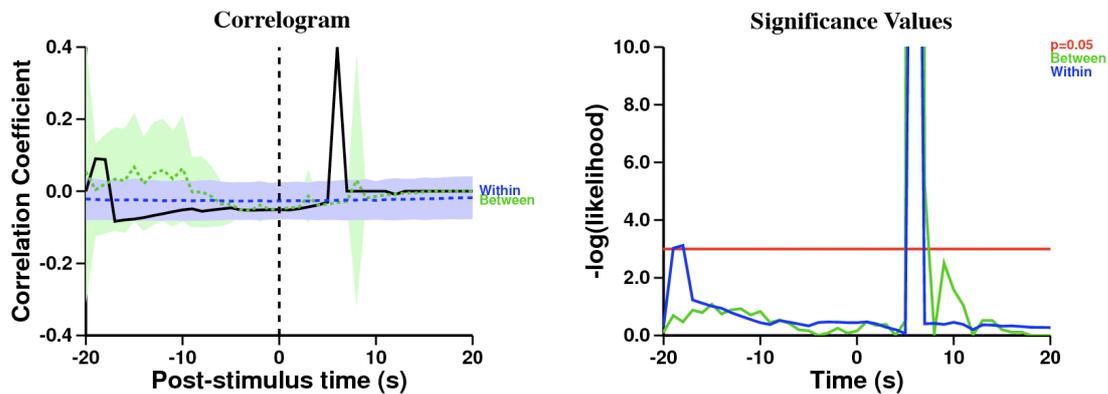


FIGURE 5.78: Referent behaviour: both chimpanzees *converging*. Target behaviour: subordinate stops walking for five seconds. After the chimpanzees were in different quadrants and walking towards the same quadrant, the subordinate stopped walking significantly more than expected from the within-trial shuffled control (peak at time= +6, $r = 0.4947$, $n = 142$; $-\log\text{-likelihood} = 36.9822$, $p < 0.05$).

3. Phase 2

In Phase 2 there is a slightly different pattern: though the data are not significant, when the chimpanzees were in different quadrants it appears that they walked towards different quadrants, and only walked towards the same quadrant much later (18 seconds) (Figure 5.79).

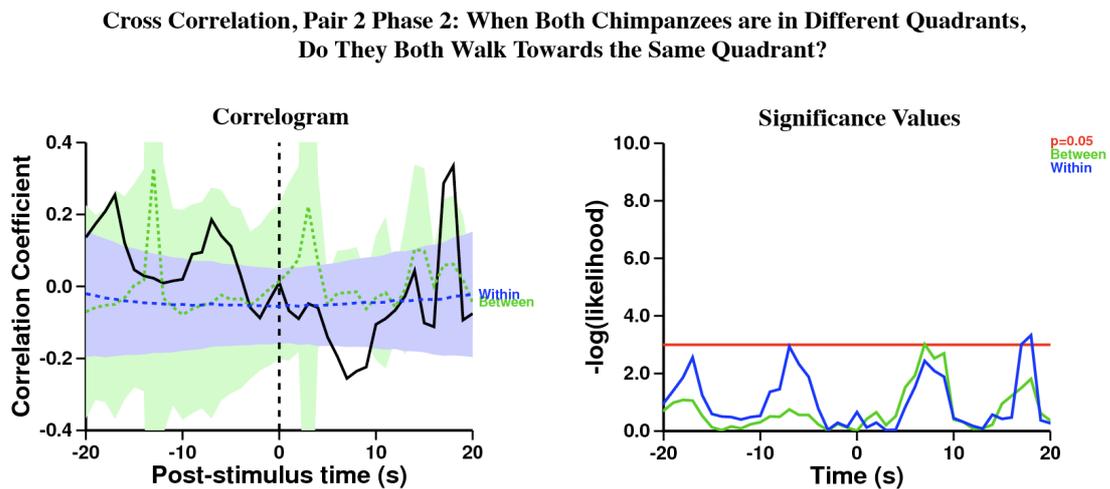


FIGURE 5.79: Referent behaviour: both chimpanzees are in different quadrants. Target behaviour: both chimpanzees walking towards the same quadrant. After both chimpanzees were in different quadrants, they did not walk towards the same quadrant (peak at time= +7, $r = -0.2557$, $n = 81$; $-\log\text{-likelihood} = 2.4353$, *ns*), but many seconds later, they did walk towards the same quadrant (peak at time= +18, $r = 0.3350$, $n = 29$; $-\log\text{-likelihood} = 3.3286$, $p < 0.05$). Before both chimpanzees were in different quadrants (before time= 0), they walked towards the same quadrant (time= -17, $r = 0.2542$, $n = 32$; $-\log\text{-likelihood} = 2.5579$, *ns*. time= -7, $r = 0.1856$, $n = 81$; $-\log\text{-likelihood} = 2.9382$, *ns*).

4. Phase 3

During Phase 3, at the moment that the chimpanzees were in different quadrants, they did not walk towards the same quadrant; only several seconds later did they start to *converge* (Figure 5.80).

Cross Correlation, Pair 2 Phase 3: When Both Chimpanzees are in Different Quadrants,
Do They Both Walk Towards the Same Quadrant?

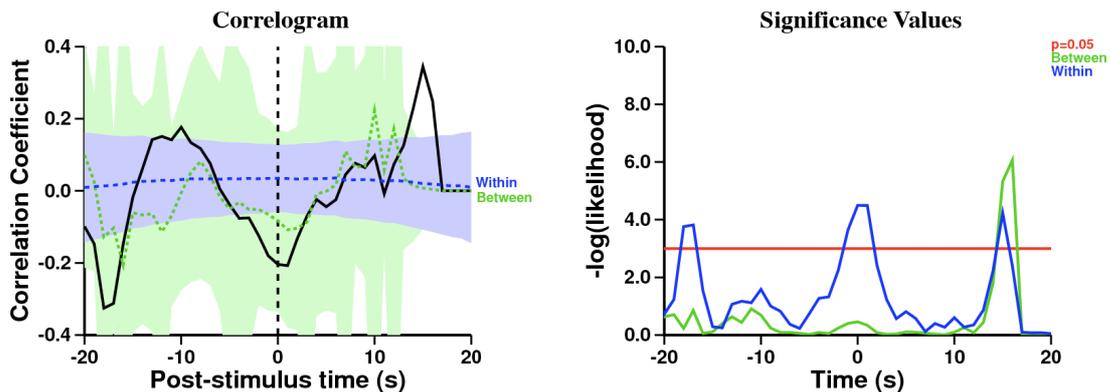


FIGURE 5.80: Referent behaviour: both chimpanzees are in different quadrants. Target behaviour: both chimpanzees walking towards the same quadrant. At the moment that the chimpanzees were in different quadrants, they did not walk towards the same quadrant (peak at time= 0, $r = -0.2040$, $n = 171$; $-\log\text{-likelihood} = 4.4959$, $p < 0.05$), but several seconds later, the chimpanzees walked towards the same quadrant significantly more than expected from the within-trial shuffled control (peak at time= +15, $r = 0.3444$, $n = 50$; $-\log\text{-likelihood} = 4.2310$, $p < 0.05$). Before the chimpanzees were in different quadrants, they appeared to walk towards the same quadrant, though this relationship was not significant (time= -10, $r = 0.1765$, $n = 87$; $-\log\text{-likelihood} = 1.5849$, ns). Many seconds before the chimpanzees were in different quadrants, they did not walk towards the same quadrant (peak at time= -17, $r = -0.3123$, $n = 39$; $-\log\text{-likelihood} = 3.8182$, $p < 0.05$).

The analysis of *converging* behaviour has shown differences between the three phases. Overall when the chimpanzees were in different quadrants they walked towards the same quadrant at a delay of several seconds, though in Phase 1 there was no delay—they walked significantly more than expected shortly after entering different quadrants. Both subjects paused while *converging*, which may suggest that they were reassessing their opponent's direction of movement.

5. No Knowledge controls

Converging behaviour was the opposite from the *Competition* trials in the *No Knowledge* controls: at the moment that the chimpanzees were in different quadrants, they walked towards the same quadrant; however, this did not last long, as the relationship of the chimpanzees walking towards the same quadrant became significantly less than expected from the within-trial shuffled control (Figure 5.81).

Cross Correlation, Pair 2 No Knowledge: When Both Chimpanzees are in Different Quadrants, Do They Both Walk Towards the Same Quadrant?

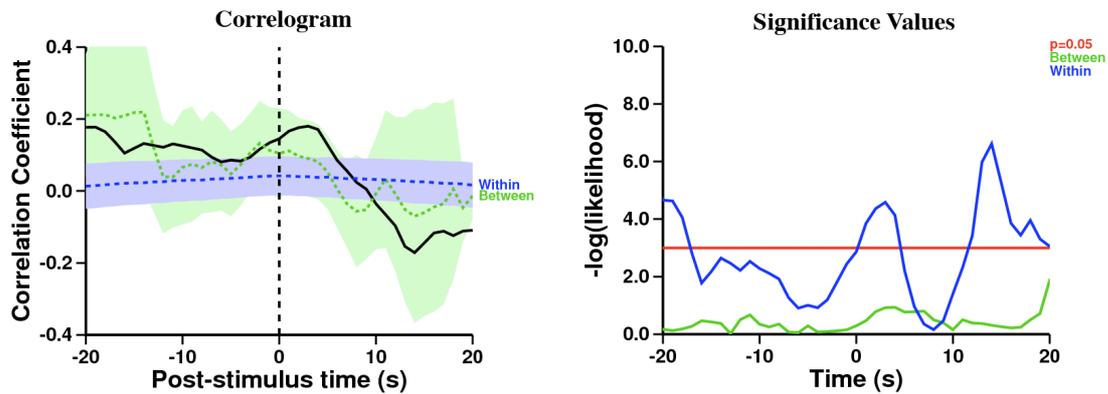


FIGURE 5.81: Referent behaviour: both chimpanzees are in different quadrants. Target behaviour: both chimpanzees walking towards the same quadrant. After the chimpanzees were in different quadrants, both chimpanzees walked towards the same quadrant significantly more than expected from the within-trial shuffled control (time= +3, $r = 0.1800$, $n = 330$; $-\log\text{-likelihood} = 4.5850$, $p < 0.05$), and then significantly less than expected (time= +14, $r = -0.1714$, $n = 269$; $-\log\text{-likelihood} = 6.6160$, $p < 0.05$).

6. Full Knowledge controls

The correlogram for the *Full Knowledge* controls suggests that the chimpanzees did *converge*, though this relationship was not significant (Figure 5.82); on those trials in which the subordinate was moving in the enclosure, she walked towards where the bait was hidden, though the dominant arrived there before her on every trial.

Cross Correlation, Pair 2 *Full Knowledge*: When Both Chimpanzees are in Different Quadrants, Do They Both Walk Towards the Same Quadrant?

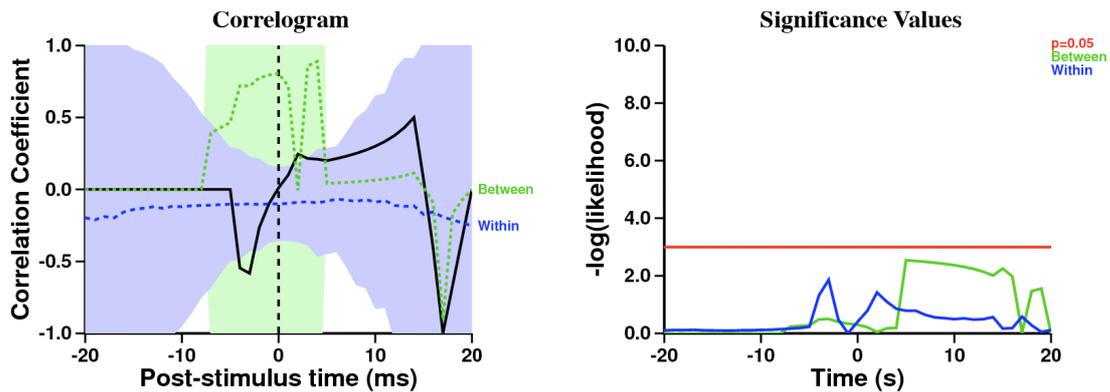


FIGURE 5.82: Referent behaviour: both chimpanzees are in different quadrants. Target behaviour: both chimpanzees walking towards the same quadrant. When both chimpanzees were in different quadrants, they walked towards the same quadrant (time= +2, $r = 0.2453$, $n = 25$; $-\log\text{-likelihood} = 1.4205$, *ns*). Before they were in different quadrants, they did not walk towards the same quadrant (time= -3, $r = -0.5831$, $n = 22$; $-\log\text{-likelihood} = 1.8595$, *ns*).

7. *No Bait, No Knowledge* controls

On the *No Bait, No Knowledge* controls, the chimpanzees did not walk towards the same quadrant, whether or not they were in the same or different quadrants (Figure 5.83).

Cross Correlation, Pair 2 *No Bait, No Knowledge*: When Both Chimpanzees are in Different Quadrants, Do They Both Walk Towards the Same Quadrant?

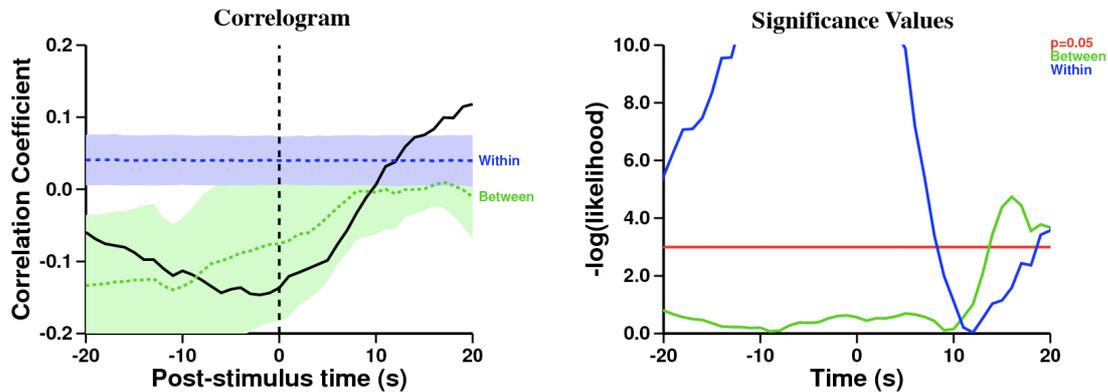


FIGURE 5.83: Referent behaviour: both chimpanzees are in different quadrants. Target behaviour: both chimpanzees walking towards the same quadrant. Both before and after the chimpanzees were in different quadrants, both chimpanzees walked towards the same quadrant significantly less than expected from the within-trial shuffled control between time = -20 and +8 (peak at time = -2, $r = -0.1465$, $n = 924$; $-\log\text{-likelihood} = 16.7791$, $p < 0.05$). After spending many seconds in different quadrants, the chimpanzees walked towards the same quadrant (peak at time = +20, $r = 0.1180$, $n = 830$; $-\log\text{-likelihood} = 3.5712$, $p < 0.05$).

8. Summary of *Convergence* behaviour

Though *converging* behaviour was different between the three phases, the overall *Competition* dataset indicates that the chimpanzees did *converge* on each other's destination. In Phase 1, the chimpanzees did *converge*; in Phases 2 and 3, they did not *converge* until they had been in different quadrants for several seconds. In the *No Knowledge* controls, the chimpanzees did *converge* very briefly, and then were significantly unlikely to do so. Furthermore, they did not *converge* in the *No Bait, No Knowledge* controls, whereas they did walk towards the same quadrant from different quadrants when they both had *Full Knowledge* of where the bait was hidden.

VI. Discussion: Pair 2

It is clear that the dominant exploited the subordinate's foraging success: the dominant was successful in finding the bait on many trials, and though she did not use the

specific cue of the subordinate walking towards the bait to inform her own search, it might have been possible that the dominant was relying on some other cue, e.g., an olfactory cue. But on closer inspection, it appeared that the two chimpanzees did walk towards the same absolute quadrants at the same time, and that the dominant's movement towards three of the four quadrants was motivated by the subordinate initially moving in those directions, regardless of the position of the bait.

TABLE 5.8: Overall summary of different following types throughout the experiment, Pair 2 (Results listed in Prediction/Outcome format)

	Overall <i>Competition</i>	Phase 1	Phase 2	Phase 3	<i>No Knowledge</i>	<i>Full Knowledge</i>	<i>No Bait, No Knowledge</i>
Dominant <i>Approaches</i> Subordinate	Yes/Yes	Yes/Yes	Yes/Yes	Yes/No	No/Yes	No/Insufficient Data	No/No
Subordinate <i>Approaches</i> Dominant	No/Yes	No/Yes	No/No	No/No	No/No	No/Insufficient Data	No/Yes
Dominant in Subordinate's <i>Footsteps</i>	Yes/Yes	Yes/Yes	Yes/Yes	Yes/No	No/No	No/Insufficient Data	No/Yes
Subordinate in Dominant's <i>Footsteps</i>	No/No	No/No	No/No	No/Yes	No/No	No/Insufficient Data	No/No
<i>Convergence</i>	Yes/Yes	Yes/Yes	Yes/No	Yes/Yes	No/No	Yes/Yes	No/No

I examined three different definitions of following behaviour: *approach*; walking in the other's *footsteps*; and *converging* on the other's destination (Table 5.8). The results show that, as expected, the dominant exploited the subordinate's foraging success, in this case from the very first trial. In the first phase the dominant used all three movement following types but had limited success in exploiting the subordinate: the dominant followed in the subordinate's *footsteps*, and when the subordinate entered another quadrant, the dominant *approached* her, but when the dominant *approached*, the subordinate stopped walking, and this tactic functioned to withhold information from the dominant. On occasion the subordinate took an indirect route while walking to the bait, or delayed walking to the bait as the dominant eagerly searched the enclosure. On trial 5, the dominant *converged* on the subordinate's destination, arriving just seconds too late to reach the reward. The dominant also *converged* on trial 10, but again the subordinate was successful in obtaining the reward. Both individuals paused while *converging* and the dominant frequently glanced at the

subordinate and readjusted her movement to match the subordinate's direction (see Chapter 6: Gaze Following). The subordinate delayed picking up the reward until after the dominant had walked sufficiently far past it.

In Phase 2, the subordinate walked more directly to the food reward, and often ran. For the first two phases of the *Competition*, the dominant moved to be closer to the subordinate more than the subordinate moved to be closer to the dominant: the dominant *approached* and followed in the subordinate's *footsteps* in Phases 1 and 2, whereas the subordinate only *approached* the dominant in Phase 1, but not in Phase 2, and did not follow in her *footsteps* in this time period. Phase 2 was the only phase in which the chimpanzees did not *converge* until much later after entering different quadrants. The correlograms for *footsteps* behaviour indicate that the chimpanzees were 'taking turns' following their competitor, thus representing in graph form the interaction in which the dominant 'followed from in front' (Stueckle & Zinner, 2008): the dominant followed, then ran ahead of the subordinate, and finally the subordinate overtook the dominant to run to the reward. When the dominant *approached*, the subordinate stopped and only on these trials in which the subordinate hesitated to walk towards the food did the dominant successfully exploit her.

In Phase 3, both subjects' behaviour changed: the dominant, who had before *approached* and followed in the subordinate's *footsteps*, no longer did. During this phase, the subordinate alternated her tactics between walking directly and delaying walking towards the hidden food, so the dominant could not use the *footsteps* tactic successfully. Rather, the subordinate started following in the dominant's *footsteps*. The reason for this was apparently that the dominant was so motivated to search that she often ran ahead of the subordinate, and unlike during the previous phases no longer waited for the subordinate to catch up, thus giving the appearance that the subordinate followed behind the dominant; though it would be more correct to say that the dominant followed from in front of the subordinate (Stueckle & Zinner, 2008). The chimpanzees continued their overall pattern of *converging*, though this was different from the previous phase.

I did not expect to observe any following behaviour in the *No Knowledge* control, since neither chimpanzee saw the baiting procedure (where before the dominant could see through the mesh adjoining their cages that the subordinate was looking through her window outside to the enclosure as the experimenter hid the bait). The dominant was nonetheless motivated to search for the banana; after all, not witnessing the baiting procedure on previous

Competition trials had not stopped her from successfully finding the food on nine occasions. The dominant did *approach* the subordinate, but did not use any other movement type, and the subordinate did not use any following type.

The dominant ran quickly on four very short trials of the *Full Knowledge* control, thus there were insufficient data in the *Full Knowledge* controls to show whether the chimpanzees *approached* or followed in each other's *footsteps*; the chimpanzees did *converge*.

The *No Bait, No Knowledge* controls were implemented to determine if the dominant would continue to approach the subordinate when no banana was hidden in the enclosure. While she did not *approach* as she had done in the original *No Knowledge* controls, she did follow in the subordinate's *footsteps*, and the subordinate *approached* the dominant. It could be the case that the chimpanzees learned over numerous trials that a banana was usually hidden in the enclosure, and that searching despite not knowing its location could be a useful strategy. Additionally, though a banana was not hidden, an experimenter did enter the enclosure as if to hide something, so the chimpanzees may have searched because they had made the association between researchers in the enclosure and hidden food items.

VII. Following Discussion for Both Pairs

My analysis using cross correlations allows me to show the “continuous feedback” between two chimpanzees as they search for a hidden food item (Menzel, 1974, p. 134). The ignorant dominant learned to exploit the informed subordinate by following to take the food (Pair 1) or by running ahead of the subordinate's path to search for the hidden food (Pair 2). This supports previous studies of producer/scrounger models that demonstrated that high rank individuals are capable of using their dominance to exploit the foraging success of subordinate producers (Baker et al., 1981; Rohwer & Ewald, 1981; Barta & Giraldeau, 1998).

Specifically, I showed that the ignorant dominant chimpanzee in each pair used three types of following to exploit her competitor: *approach*; *footsteps*; and *converge*. The correlograms showed marked differences in the dominants' behaviour for each type of following across the three phases of the *Competition*, as well as for each of the control conditions. During all phases of the *Competition* the ignorant dominants followed the subordinates using at least one movement type that I defined, indicating that they were relying on their informed subordinate partners to produce the food, which they were able to do because of the privileged information they had. On the other hand, the dominants did not

follow the subordinates using any type when they had seen where the food was hidden during the baiting process in the *Full Knowledge* control. In the *No Knowledge* and *No Bait, No Knowledge* controls, though the subordinates were also ignorant of the food's location, the dominants did not stop using their previously successful tactics, and at least for the dominant of Pair 2, the tactic of searching extensively through the enclosure led to success in obtaining food.

There were similarities and differences between the two pairs' interactions. One major difference was in the manner that the dominants obtained food: the dominant of Pair 2, Georgia, was very keen to search for the hidden banana and would frequently run ahead of her informed partner, Reinette, in order to expand her search area in an attempt to find the food before Reinette found it, whereas in Pair 1, the dominant Rita won the banana on a few trials because the subordinate Missy uncovered the reward and either walked away from it or sat next to it and allowed Rita to take it. In both pairs, the subordinate subjects adjusted their behaviour in response to the dominant's exploitation, for example by delaying their approach to the food. For both pairs, the dominants then changed their tactics in reaction to the subordinates' movement (or pauses) in the enclosure. However, the trajectory of the subordinates' tactic of delaying the approach to the food was different between the pairs: the subordinate of Pair 2 employed this tactic almost immediately, whereas the subordinate of Pair 1 did not. This was most likely due to the fact that the subordinate of Pair 1 did not experience the same degree of exploitation pressure from the dominant until many trials into the *Competition*.

One observation that should be noted is that on many trials in which either subordinate delayed her approach to the hidden food, or took an indirect route to the hiding place, her behaviour functioned to tactically deceive her dominant partner. On a behavioural level, the subordinate may have learned over repeated trials that when the dominant followed her closely, she was more likely to be exploited by the dominant, and so the subordinate acted simply to avoid her dominant partner. These instances are similar to those reported in many other studies (Menzel, 1974; Coussi-Korbel, 1994; Held et al., 2000, 2002, 2010; Hare et al., 2001, 2003; Hirata & Matsuzawa, 2001; Ducoing & Thierry, 2003, 2004; Bugnyar & Kotrschal, 2004; Schloegl et al., 2008b). Tactical deception is often considered a good place to seek strong evidence of second-order intentionality (Mitchell, 1986; Whiten & Byrne, 1988). Interpreted in more cognitive terms, the subordinate in each pair withheld information

or provided false information by misleading her opponent away from the food, causing the dominant to falsely believe that the subordinate did not know where the food was or that it was in a different location; upon abandoning her search to return to the start cages, the dominant often turned around at just the right moment to witness the subordinate picking up the food. While the subordinate's tactical deception (in this case, analysed as a stop in locomotion for five seconds) clearly depended on the cue of the dominant following in some way (e.g., the subordinate of Pair 1 did not delay walking towards the bait in Phase 1 before the dominant partner started using a following type), it may involve more cognitive abilities than simple associative learning. For example, the subordinate must inhibit her immediate desire to obtain the banana, and understand that by walking in the wrong direction, the dominant partner will continue to follow, and be deceived (Güzeldere et al., 2002; Bugnyar & Kotrschal, 2004). While instances of tactical deception raise interesting questions about intentionality and theory of mind in great apes, the most parsimonious explanation is a sophisticated behavioural explanation, couched in an intentional stance and cognitive framework (Byrne & Whiten, 1991; Byrne, 1997; Byrne & Bates, 2006): the subordinates acted intentionally to prevent the dominants from getting near the bait by delaying their own approach to the food, thus acting to achieve their ultimate goal of obtaining the hidden food reward.

The dominants' use of three types following behaviour as an exploitative tactic raises questions about which behavioural cues in the subordinate the dominant was using to alter her own behaviour. Especially in the case of *converging*, the dominant must not only observe a movement cue, as in the *approach* and *footsteps* types, but must also take the geometric perspective of the subordinate in order to adjust her own movement to form a route that intersects with the subordinate's. It would seem that using the subordinate's visual perspective as a cue would support the dominant's ability to *converge* (Tomasello et al., 1999). Being able to use gaze cues may play an important role in this study: since the subordinate sees, and therefore knows (Hare et al., 2001), where the bait is hidden, one would expect her to gaze towards the bait as she searches for it. Chimpanzees consistently follow group members' gaze (Tomasello et al., 1998), and a theory of mind-type explanation of searching behaviour would predict that the dominant should follow the subordinate's gaze in order to gain information about the location of the hidden food, since the dominant saw through the cage mesh that the subordinate watched the baiting procedure through her

window; the dominant knows that the subordinate knows where to find the banana. Evidence of similar patterns in gaze following as in movement following (i.e., that the dominant follows the subordinate, but not the reverse), would support the hypothesis that the dominant is using the subordinate's gaze cue to inform her search for the bait (see Chapter 6: Gaze Following).

The next chapter will approach the analysis of gaze following in a similar manner to movement following by analysing how subjects follow each other's gaze, which partner's gaze is contingent on the other's, and how gaze patterns change over the course of the *Competition* and between different control conditions.

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I. Abstract

Gaze following is a process by which one can gain information about another individual's attention; this analysis explores whether an ignorant chimpanzee competitor can obtain valuable information regarding the location of a hidden food item by following an informed conspecific opponent's gaze. I used cross correlations to examine how each chimpanzee competitor in the informed forager paradigm used two types of gaze following: *static* gaze following; and following a change in gaze direction, i.e., a *gaze onset*. I showed that contrary to predictions from the social attention hypothesis, ignorant dominants were more likely to follow informed subordinates' *static* gaze and *gaze onset* than the reverse, suggesting that gaze must be interpreted in the context of what each competitor knows about the location of the hidden bait. I compared the use of the two gaze types with three different movement types, *approach*; *footsteps*; and *converge*; to assess whether visual information gained through following a competitor's gaze can be integrated to modify one's own competitive tactic. Results showed that in Pair 1, only the dominant Rita followed the subordinate Missy's *static* gaze to adjust her movement direction while *converging*, and each subject followed her opponent's *gaze onset* while following in her *footsteps*, indicating that changes in gaze direction are more salient in close proximity, as they may predict a change in body direction. In Pair 2, the dominant Georgia followed the subordinate Reinette's *static* gaze while *converging*, and used both gaze types when *approaching*. The dominant alternated between gazing towards the same and towards a different quadrant as the subordinate while following in her *footsteps*, which reflects the dominant's tendency to alternate between the leader and follower position while using that movement type. When experiencing strong exploitation pressure from her dominant competitor, each subordinate was capable of withholding her gaze cue towards the bait, which functioned to deceive the opponent, suggesting that chimpanzees may understand that their gaze direction can reveal their desires or intentions to other individuals. This is the first detailed analysis of both types of gaze described for a naturalistic foraging competition. Results may elucidate chimpanzee-typical gaze patterns as well as how different individuals use gaze to gain information in social situations.

II. Introduction

The ability to follow another individual's direction of gaze to a point in space is an important mechanism for gaining information from others about elements in the physical and social environment. Emery (2000) defines gaze following as noticing another individual's direction of attention to a point in space, and then adjusting one's own line of regard to the same point in space; when an object or other focus of attention is present at that point, the two individuals have joint attention on that object. Many primate species have been shown to follow the gaze of their conspecifics and/or human experimenters (see Emery, 2000 for a review), raising the question of what information can be obtained from the gaze interaction; additionally the question remains as to whether gaze is an automatic response or is motivated by deliberate information-seeking.

Some studies note that in the absence of clear eye-direction cues, quadrupedal body orientation and/or head orientation are often sufficient communicative cues to indicate one's direction of attention (Emery, 2000; Langton et al., 2000; Kaminski et al., 2004), and that these cues may be more available or salient to group members in a variety of situations. Non-human primate eyes have dark pigmented sclera, making gaze difficult to determine based on the direction of the pupil/iris in the skull (Kobayashi & Kohshima, 2001), yet Bethell et al. (2007) have shown that chimpanzee gaze originating from the direction of the eyes, as contrasted with head orientation, can be detected by human observers, and may hold signal value to conspecifics. For the purpose of this analysis of chimpanzee gaze in a naturalistic foraging situation, I coded head direction, rather than eye direction, as a proxy for gaze direction, because it was more often visible from observation and because many studies have shown that non-human primates visually orient to the direction of the head, rather than body, when the two were incongruent (Hietanen, 2002; Kaminski et al., 2004; Seyama & Nagayama, 2005; Shepherd & Platt, 2008), and are more successful in following head orientation than eye gaze (Povinelli & Eddy, 1996a; Kaminski et al., 2004; Tomasello et al., 2007).

In experimental situations, chimpanzees are capable of following a human demonstrator's gaze, even around opaque barriers (Call et al., 1998; Tomasello et al., 1999). However, chimpanzees have little success in using a human experimenter's communicative gaze cue to locate hidden food, often relying on a body posture or head orientation cue (Povinelli & Eddy, 1996; Reaux et al., 1999; Bulloch et al., 2008; Tomasello et al., 2007).

Chimpanzees are more skilful in competitive than cooperative interactions (Hare & Tomasello, 2004) and a series of experiments (Hare et al., 2000, 2001) has shown that chimpanzees do have an understanding of what conspecific competitors have seen during a recent baiting procedure. During these studies, a subordinate subject was informed of the location of a hidden food item, and competed with a dominant that was either uninformed or misinformed of the correct location of the food. Results suggested that the subordinate subjects knew what their competitors knew—i.e., what they had seen, and importantly, what they had not seen, during baiting. In more naturalistic foraging situations, following conspecific gaze may be beneficial in order to locate a food patch (Hare et al., 2000; Schloegl et al., 2007; Zuberbühler, 2008; Rosati & Hare, 2009).

The current study aimed to expand the work by Hare and colleagues by addressing *how* chimpanzees know what they appear to know about others, based on what they have seen, using Menzel's (1974) informed forager paradigm. Gaze following is generally considered a precursor to human-like theory of mind, as it is a process by which one can gain information about another individual's attention (Baron-Cohen, 1991; Gómez, 1991; Whiten & Byrne, 1991; Whiten, 1997; Emery, 2000, Bulloch et al., 2008; Zuberbühler, 2008). If chimpanzees, in particular an ignorant dominant competitor, can obtain valuable information regarding the location of a hidden food item by following gaze, there should be evidence that the ignorant opponent follows the informed subject's gaze. Menzel originally described how his chimpanzee subject's gaze orientation influenced his subsequent searching behaviour: the dominant "oriented repeatedly at Belle [the informed subordinate] and adjusted his place of search appropriately if she showed any signs of moving or orienting in a given direction" (Menzel, 1974, p. 135). Additionally, as many examples of tactical deception have been reported in this paradigm (Menzel, 1974; Coussi-Korbel, 1994; Held et al., 2000, 2002; Hare et al., 2001; Hirata & Matsuzawa, 2001; Hare et al., 2003; Ducoing & Thierry, 2003, 2004; Bugnyar & Kotrschal, 2004; Schloegl et al., 2008b; Held et al, 2010), this study sought to investigate whether informed subjects can withhold gaze cues (similar to Goodall, 1971) as a deceptive tactic. Tactical deception is often considered a good place to seek strong evidence of second-order intentionality (Mitchell, 1986; Whiten & Byrne, 1988); hence, using gaze following, or gaze withholding, may provide additional evidence to support the hypothesis that chimpanzees know what others know, based on what they have seen.

Furthermore, being able to assess a competitor's gaze direction may play a role in altering one's own movement, yet “there are no studies that investigate experimentally whether particular primate species use the gaze direction of conspecifics as a cue to their impending behaviour, and there is only indirect evidence that they use conspecifics' bodily orientation as a cue to their direction of travel” (Tomasello & Call, 1997, p. 358). Many examples from previous studies provide this indirect evidence: Menzel wrote that the informed subordinate Belle waited “until Rock [the ignorant dominant] looked in the opposite direction before she moved toward the food” (Menzel, 1974, p. 135). Hirata and Matsuzawa describe a similar episode, “Chloe [informed] initiated the exchange of glances with Pendesa [ignorant] before proceeding to an empty container” (Hirata & Matsuzawa, 2001, p. 292); and Coussi-Korbel wrote that the subordinate “glanced back to his group members as if to make sure that Boss [ignorant dominant] was following him” (Coussi-Korbel, 1994, p. 169). All of these records suggest that it is worthwhile to explore questions related to how the subjects adjust their movement, and what they stand to gain by paying attention to the direction of their competitor's gaze.

An in-depth and detailed analysis of two distinct types of gaze following will expand our knowledge of which gaze cues elicit following (static or dynamic), whether both subjects follow the other's gaze, and particularly what information can be obtained from gaze interactions. Using a new method of statistical analysis, cross correlation, will improve our understanding of the timing and contingencies between subjects' actions. For the informed forager paradigm, differences between the subjects' gaze following can be interpreted in the context of what each opponent knows about the other's knowledge. I predicted that ignorant dominants would follow the gaze of informed subordinates in order to gain information regarding the location of the hidden food, whereas subordinates would not follow the gaze of dominants. I predicted that gaze following would be closely linked with movement following, and that either process would influence the other.

A. *Static* Gaze Following

As in Emery (2000), I define *static* gaze following as: “one individual looks at the other, and then both subjects gaze towards the same quadrant of their enclosure.” This definition does not specify an object of attention that the chimpanzees may be looking at together (joint attention). Nor does the definition necessarily require either chimpanzee to change her direction of gaze. For example, the dominant could be walking in the

subordinate's *footsteps* (see Chapter 5: Movement Following), and both chimpanzees could be looking straight ahead towards the same quadrant; in that moment, the dominant is looking at the subordinate *and* towards the same quadrant as the subordinate. One constraint of the definition is that because gaze direction is not specific to an object, both chimpanzees may be looking towards the same quadrant, but to different locations/objects within that quadrant. As with movement following, this is as specific as I could define gaze direction without either making assumptions about which object (among many scattered in each quadrant) that a subject was looking at, or without losing valuable data by too broadly generalising gaze as towards or away from the bait.

B. Following Gaze Onset

A different gaze cue that I analysed is following the *onset* of a gaze, a change towards a new direction. I defined following gaze *onset* as: "one individual changes her gaze direction while in view of the other, and then both subjects gaze towards the same quadrant." The individual that changes her gaze should be in the other's potential field of vision (i.e., not behind the other, or hidden behind a barrier), but the other does not necessarily have to be looking directly at the individual at the time she changes her gaze.

This chapter examines whether each chimpanzee follows the gaze of their opponent, and whether a change in gaze, i.e., a gaze *onset*, is a more salient cue than *static* gaze direction. For each type of gaze following, cross-correlograms and $-\log$ -likelihood graphs are presented for the entire *Competition* dataset, the *No Knowledge*, *Full Knowledge*, and *No Bait*, *No Knowledge* controls. The pattern of gaze following for each definition is essentially the same across the three phases, so graphs from each phase are included in the appendix to Chapter 6.

III. Results: Pair 1, Missy and Rita

First I present the general patterns of both chimpanzees gazing towards the bait, and then gazing towards absolute locations (i.e., towards quadrants 1, 2, 3, 4). I then present an analysis of each subject's use of the two defined gaze following types, and how they relate to the three movement following types defined in Chapter 5. The questions that will be addressed include: Did the dominant gaze towards the bait after the subordinate gazed towards the bait, and does this pattern extend to other areas of the enclosure? Did the dominant follow the subordinate's *static* gaze, or her gaze *onset*, and did the subordinate use

these gaze types to follow the dominant's gaze? Does gaze following lead to movement following, or the other way around?

A. Analysis of Gazing Towards the Bait During *Competition*

The subordinate Missy saw where the bait was hidden on each trial, but the dominant Rita did not. I use cross correlations to address both chimpanzees' gaze towards the hidden bait (the analysis of gazing towards the bait for Pair 1 is covered in greater detail in Chapter 4: Statistical Methods as an illustration of how the cross correlation method works). I address the hypothesis that the knowledgeable subordinate's gaze direction influences the ignorant dominant's gaze direction by asking, "When the subordinate gazes towards the bait, does the dominant gaze towards the bait?" (Figure 6.1; graphs for *No Knowledge* and *Full Knowledge* controls are included in the appendix).

After the subordinate gazed towards the bait, the dominant gazed towards the bait significantly more than expected from the within-trial shuffled control. Before the subordinate started gazing towards the bait, the dominant gazed towards the bait significantly less than expected from the within-trial shuffled control.

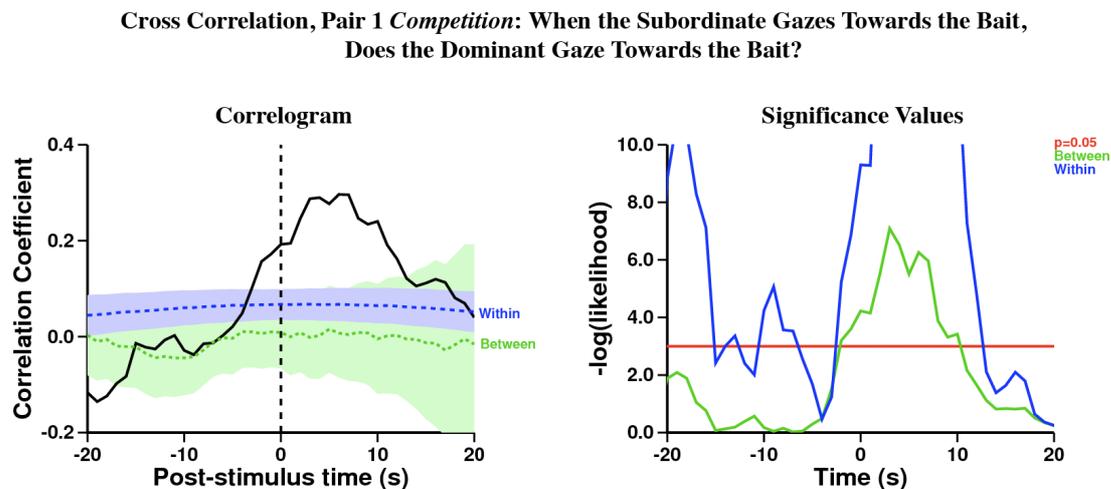


FIGURE 6.1: Referent behaviour: subordinate gazing towards the bait. Target behaviour: dominant gazing towards the bait. After the subordinate gazed towards the bait, the dominant gazed towards the bait significantly more than expected from the within-trial shuffled control (peak at time= +4, $r = 0.2897$, $n = 777$; $-\log\text{-likelihood} = 23.6418$, $p < 0.05$). Before the subordinate started gazing towards the bait, the dominant was significantly unlikely to gaze towards the bait (peak at time= -19, $r = -0.1356$, $n = 610$; $-\log\text{-likelihood} = 10.8636$, $p < 0.05$).

The dominant followed the subordinate's gaze towards the bait, but perhaps there was something different about the subordinate's gaze cue towards the bait, e.g., more emphatic,

that encouraged the dominant to follow her gaze in that direction. To address this question, I analysed whether the dominant followed the subordinate's gaze to absolute directions in their enclosure, regardless of the location of the hidden bait.

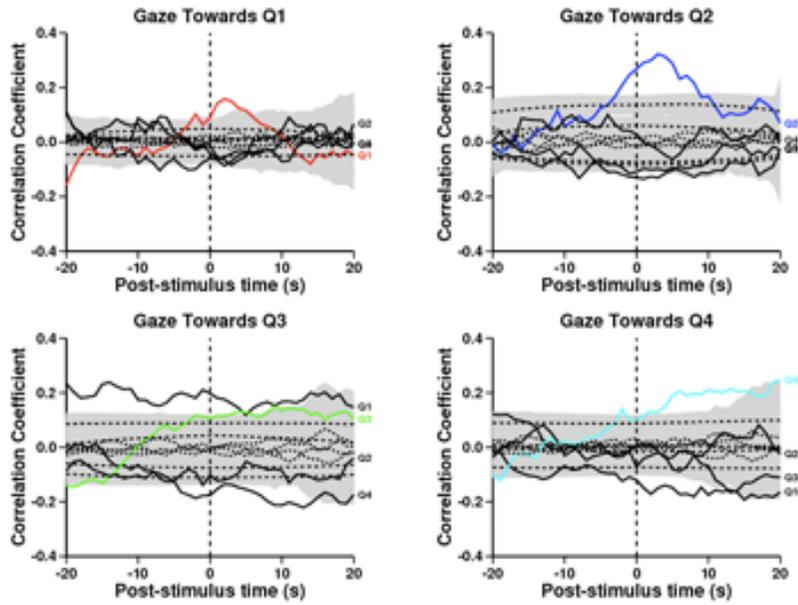
B. Analysis of Gazing Towards Absolute Directions During *Competition*

To examine whether there is some inherent cue in gazing towards the bait that makes the gaze more salient, and more likely to be followed, I analysed whether the dominant and the subordinate gazed to absolute locations in the enclosure at the same time, regardless of the location of the bait. I asked, "When the subordinate gazes towards a quadrant, towards which quadrant does the dominant gaze?" I compared the subordinate's gaze towards one quadrant with the dominant's likelihood of gazing towards any of the four quadrants (Figure 6.2). When the subordinate gazed towards Quadrant 1 and Quadrant 2, the dominant was significantly likely to gaze toward the *same* quadrant, rather than any other quadrant when compared to the between-trial shuffled control. This particular control is used because the data are coded in absolute terms (i.e., towards quadrants 1, 2, 3, 4): the chimpanzees were in a differently numbered quadrant on each trial, so shuffling between trials eliminated contingent relationships but maintained sequences of behaviour (see Chapter 4: Statistical Methods). When the subordinate gazed towards Q4, the dominant also gazed towards Quadrant 4, more than any other quadrant, and this relationship trended towards being significantly more than expected from the between-trial shuffled control. There was a different pattern for Q3: when the subordinate gazed towards Q3, the dominant was more likely to gaze towards Q1. Thus for three quadrants, both chimpanzees gazed towards the same absolute direction at the same time, when the location of the bait was not taken into account. The different pattern in Q3 may be an artefact of the experimental setup and layout of the enclosure: the dominant entered the enclosure before the subordinate, and therefore may have been gazing ahead (towards Q1) at the time that the subordinate entered and gazed to Q3. It is clear that there is a very strong influence of gazing towards Q2: the correlation coefficients for both chimpanzees gazing in that direction are much higher than for other quadrants. This may be again a result of the layout of the enclosure and the chimpanzees' pattern of movement towards it as discussed in the Chapter 5: Movement Following. The chimpanzees spend the least amount of time currently in Q2, and the most amount of time walking towards Q2.

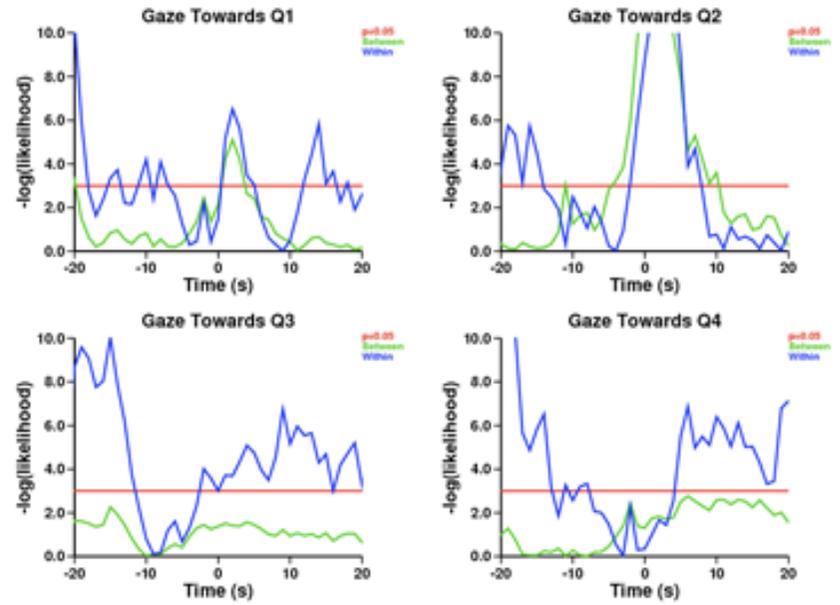
FIGURE 6.2 (next page): In each panel, the referent behaviour at time= 0 is the subordinate gazing towards the quadrant of that panel. The coloured line in each panel represents the cross correlation of the dominant gazing towards the same quadrant as the subordinate. The three solid black lines represent the cross correlation of the dominant gazing towards each of the other three quadrants. The dotted lines with the gray spread represent the within- and between-trial shuffled controls and their standard errors of the mean. For example, in the top left panel, the referent behaviour at time= 0 is the subordinate gazing towards Q1 and it is correlated with the target behaviour of the dominant gazing towards Q1, and this relationship is plotted with a red line. The black lines show the cross correlations of the subordinate gazing towards Q1 with the dominant gazing towards Q2, Q3, and Q4. As shown below, after the subordinate started gazing towards Q1 (time= +2, $r = 0.1420$, $n = 843$; $-\log\text{-likelihood} = 5.116$, $p < 0.05$), and Q2 (time= +1, $r = 0.2919$, $n = 843$; $-\log\text{-likelihood} = 12.9569$, $p < 0.05$), the dominant gazed towards the same quadrant as the subordinate significantly more than expected from the between-trial shuffled control. After the subordinate started gazing towards Q3 (time= +4, $r = 0.1314$, $n = 777$; $-\log\text{-likelihood} = 1.5722$, ns), there was no relation, and after the subordinate gazed towards Q4 (time= +6, $r = 0.2056$, $n = 732$; $-\log\text{-likelihood} = 2.7637$, ns), the dominant gazed towards the same quadrant as the subordinate; this relationship trends towards being more than expected from the between-trial shuffled control.

Cross Correlations, Pair 1 *Competition*: When the Subordinate Gazes Towards a Quadrant, Towards Which Quadrant Does the Dominant Gaze?

Correlograms



Significance Values



There was a very large effect of both chimpanzees gazing towards Q2 and the opposite pattern of the dominant gazing towards Q3 before the subordinate started gazing in that direction, so I analysed how much time each chimpanzee spent gazing towards each quadrant in their enclosure.

C. Time Spent Gazing Towards Each Quadrant During *Competition*

I calculated the percent of time that each chimpanzee spent gazing towards each of the four quadrants to determine if their gaze patterns were equally distributed throughout different areas of their enclosure or influenced by their asymmetrical movement patterns (see Chapter 5: Movement Following). Both chimpanzees gazed less frequently towards Q2 than towards the other quadrants (Table 6.1).

TABLE 6.1: Percent of time each subject gazed towards each quadrant, Pair 1

Quadrant	Missy Gaze	Rita Gaze
Q1	26.7%	28.3%
Q2	17.3%	11.9%
Q3	26.7%	33.9%
Q4	21.4%	23.1%
0 (Unknown)	7.8%	2.8%

Overall, when both subjects' gaze was recorded at the same time (70.8% of all trials), they both gazed together towards the same quadrant 32.6% of the time. Of this total time gazing towards the same quadrant (Table 6.2), they spent the largest amount of time gazing towards Q3, 39.36%. Of the total time gazing to the same place, 29.08% was to Q1. As with movement, the percentage of gaze direction indicates a side bias towards the left side of the enclosure (Quadrants 1 and 3), as the chimpanzees only gazed towards Q2 and Q4 for 14.54% and 16.67% of the time they gazed towards the same direction at the same time, respectively.

TABLE 6.2: Percent of time that both chimpanzees gaze towards each quadrant, of the overall time spent gazing together towards the same quadrant, Pair 1

Quadrant	Time
Q1	29.08%
Q2	14.54%
Q3	39.36%
Q4	16.67%
0 (Unknown)	0.35%

Both chimpanzees spent the majority of their time on the left side of the enclosure in Quadrants 1 and 3 (see Chapter 5: Movement Following), and the most time gazing towards those same quadrants. However, gaze direction was not always congruent with current location or direction of movement: the subordinate gazed to the quadrant she was currently in 39.35% of the time and towards the quadrant to which she was headed 39.24% of the time; the dominant gazed to the quadrant she was currently in 39.68% of the time and towards the quadrant to which she was headed 31.59% of the time. Both subjects' gaze was often incongruent with her direction of movement, approximately 40-50% of total recorded gazes.

Since this chapter covers gaze interactions between the two chimpanzees, it is important to note that each subject spent an approximately equal proportion of time looking at her opponent: the subordinate looked at the dominant for 28.11% of the time that her gaze direction was recorded, and the dominant looked directly at the subordinate for 32.02% of the time that her gaze direction was recorded (Subjects "looked" at specific individuals or objects, and "gazed" towards general directions in their enclosure).

Whether the chimpanzees' gazing behaviour is analysed in terms of relative position in the enclosure (e.g., towards the bait) or in terms of absolute direction (e.g., towards Q2), both chimpanzees gazed towards the same location, upon the subordinate's gaze cue at time=0. The exception was when they gazed towards Q3: when the subordinate gazed towards Q3, the dominant was more likely to gaze towards Q1, perhaps an artefact of the experimental setup as the dominant entered the enclosure before the subordinate, and may have been looking ahead of herself towards Q1. Overall, the general pattern of gazing towards the same quadrant at the same time may indicate that the ignorant dominant was following the gaze of the knowledgeable subordinate in order to obtain information about where the hidden food was located.

As this is the first detailed analysis of gaze following of its kind (in a naturalistic foraging experiment), I investigated two types of gaze following, *static* and *onset*, to determine whether certain visual cues such as a dynamic head-turn elicit gaze following more strongly than static gaze cues.

D. *Static* Gaze Following

Here I will describe whether each subject follows her opponent's *static* gaze, using cross correlation analysis. Recall that *static* gaze following is defined as "one individual looks at the other and then both chimpanzees gaze towards the same quadrant." I will first

address whether the dominant follows the subordinate's *static* gaze, and then whether the subordinate follows the dominant's, for the entire *Competition* dataset (graphs showed consistent patterns across each of the three phases, so individual Phase graphs are included in the appendix to Chapter 6), then the *No Knowledge*, *Full Knowledge*, and *No Bait, No Knowledge* controls.

1. Entire *Competition* dataset

For the entire *Competition* dataset, after the dominant looked at the subordinate, both chimpanzees gazed towards the same quadrant significantly more than expected from the within-trial shuffled control (Figure 6.3). When the subordinate looked at the dominant, both chimpanzees gazed towards the same quadrant significantly less than expected from the within-trial shuffled control (Figure 6.4). This particular control is used because the data are collapsed (same/different quadrant, rather than quadrants 1, 2, 3, 4): because the chimpanzees gazing towards "different" quadrants on trial one does not necessarily connote the same physical places as when they gaze towards "different" quadrants on trial two, a within-trial shuffle is more appropriate because it maintains the behavioural contingencies between subjects but eliminates the sequences of behaviour (see Chapter 4: Statistical Methods). Therefore, the dominant was highly likely to follow the subordinate's *static* gaze, but the subordinate was unlikely to follow the dominant's *static* gaze.

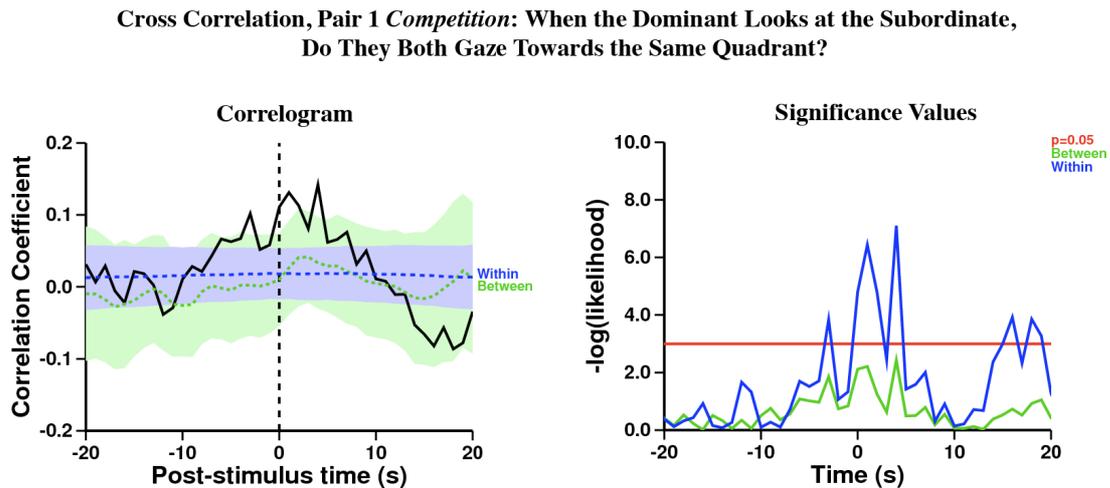


FIGURE 6.3: Referent behaviour: dominant looking at subordinate. Target behaviour: both chimpanzees gazing towards the same quadrant. After the dominant looked at the subordinate, both chimpanzees gazed towards the same quadrant significantly more than expected from the within-trial shuffled control (peak at time= +4, $r = 0.1420$, $n = 831$; $-\log$ -likelihood= 7. 1041, $p < 0.05$).

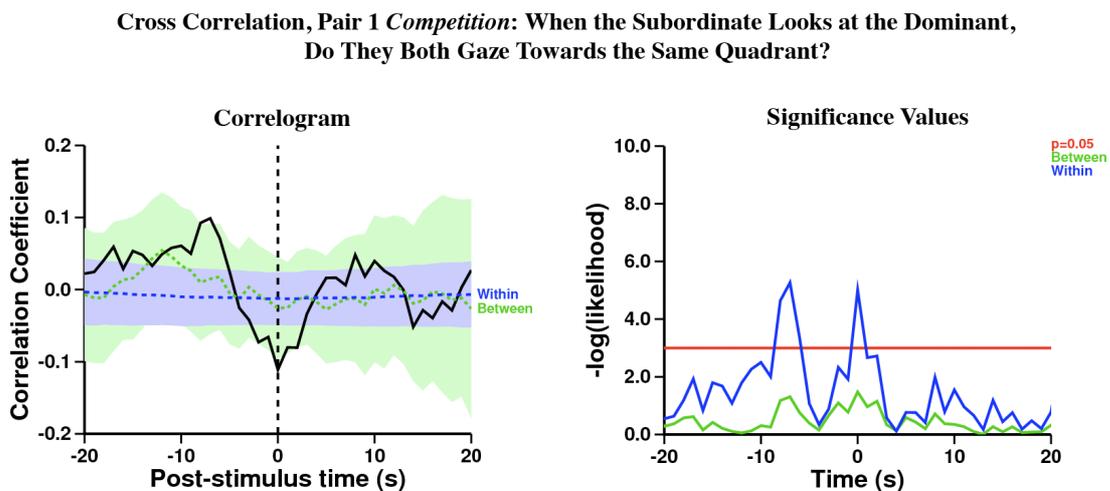


FIGURE 6.4: Referent behaviour: subordinate looking at dominant. Target behaviour: both chimpanzees gazing towards the same quadrant. At the moment that the subordinate looked at the dominant, both chimpanzees gazed towards the same quadrant significantly less than expected from the within-trial shuffled control (peak at time= 0, $r = -0.1112$, $n = 855$; $-\log$ -likelihood= 5.0108, $p < 0.05$). Before the subordinate looked at the dominant, both chimpanzees gazed towards the same quadrant (peak at time= -7, $r = 0.0988$, $n = 708$; $-\log$ -likelihood= 5.2637, $p < 0.05$).

While the percent of time that each chimpanzee spent looking at her opponent is nearly equivalent, there is clearly a much stronger effect of both subjects gazing towards the

same quadrant only after the dominant looked at the subordinate. This pattern remains consistent through all three phases (see appendix to Chapter 6).

2. *No Knowledge* controls

Since neither chimpanzee had seen where the bait was hidden in the *No Knowledge* controls, I did not expect there to be a difference between their *static* gaze following patterns. The relationship between looking at the opponent and then gazing towards the same quadrant was not significant for either subject, though for both individuals there was a trend in the data that they both followed the other's *static* gaze (Figures 6.5 and 6.6).

Cross Correlation, Pair 1 *No Knowledge*: When the Dominant Looks at the Subordinate, Do They Both Gaze Towards the Same Quadrant?

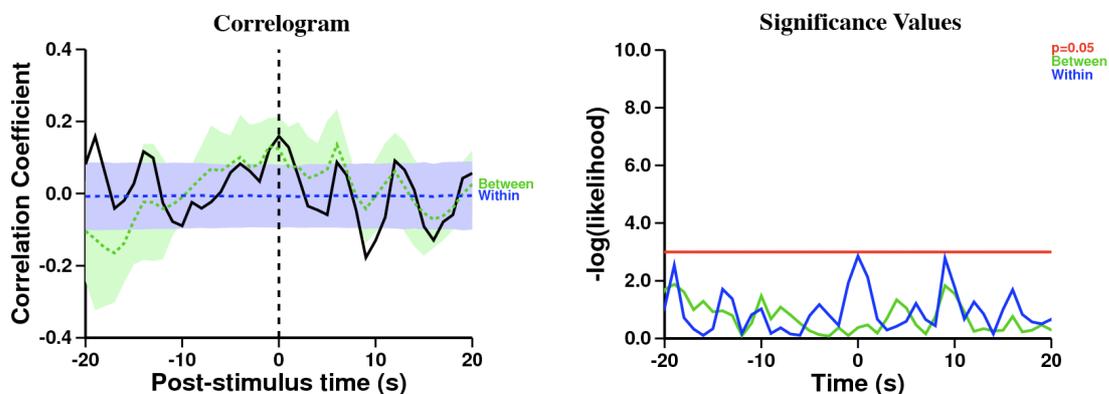


FIGURE 6.5: Referent behaviour: dominant looking at subordinate. Target behaviour: both chimpanzees gazing towards the same quadrant. After the dominant looked at the subordinate, both chimpanzees gazed towards the same quadrant; this relationship trends towards being more than expected from the within-trial shuffled control (peak at time= 0, $r=0.1591$, $n=233$; $-\log\text{-likelihood}=2.8550$, *ns*), but 9 seconds later the chimpanzees were not gazing towards the same quadrant (peak at time= +9, $r=-0.1777$, $n=181$; $-\log\text{-likelihood}=2.7848$, *ns*).

**Cross Correlation, Pair 1 No Knowledge: When the Subordinate Looks at the Dominant,
Do They Both Gaze Towards the Same Quadrant?**

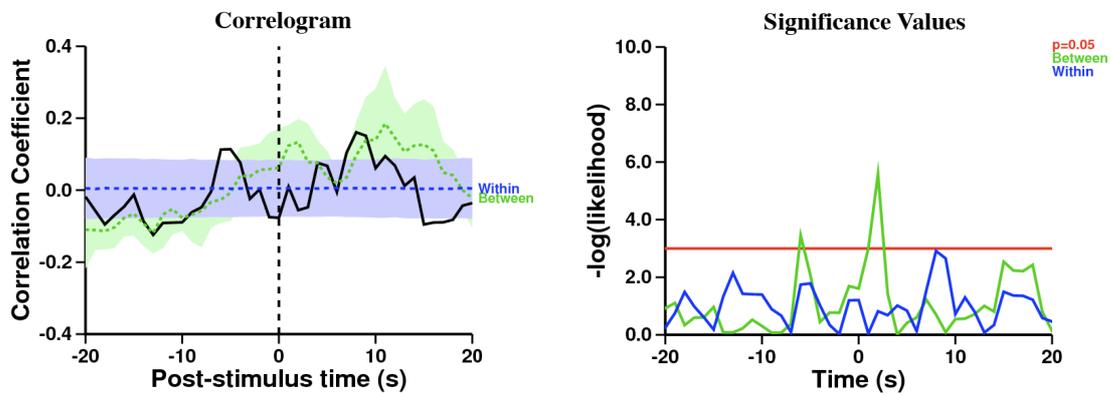


FIGURE 6.6: Referent behaviour: subordinate looking at dominant. Target behaviour: both chimpanzees gazing towards the same quadrant. After the subordinate looked at the dominant, both chimpanzees gazed towards the same quadrant; this relationship trends towards being more than expected from the within-trial shuffled control (peak at time= +8, $r=0.1609$, $n=221$; $-\log\text{-likelihood}=2.9114$, *ns*).

3. Full Knowledge controls

I did not expect the dominant to follow the subordinate's gaze in order to gain information about the hidden bait in the *Full Knowledge* controls since she had witnessed the baiting procedure; there is no relationship indicating that the dominant followed the subordinate's gaze (Figure 6.7). On these trials, the dominant either ran towards the bait to retrieve it, in which case the subordinate was behind her, or she stayed inside and did not compete for the food. Therefore, there were very few instances that the dominant looked at the subordinate.

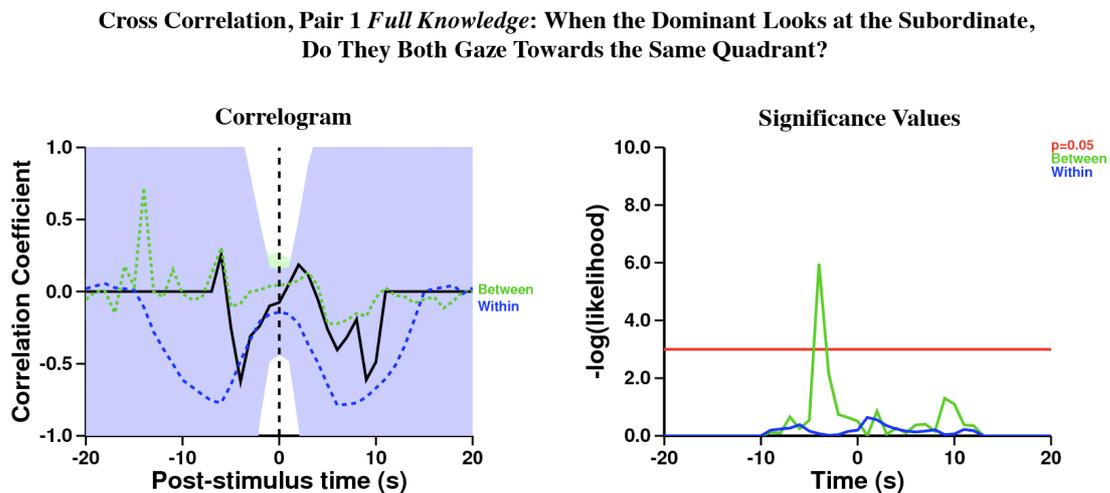


FIGURE 6.7: Referent behaviour: dominant looking at subordinate. Target behaviour: both chimpanzees gazing towards the same quadrant. There is no relation between the dominant looking at the subordinate and whether both chimpanzees gaze towards the same quadrant.

The subordinate did follow the dominant's *static* gaze (Figure 6.8). She quickly alternated between gazing towards the same quadrant as the dominant and towards a different quadrant.

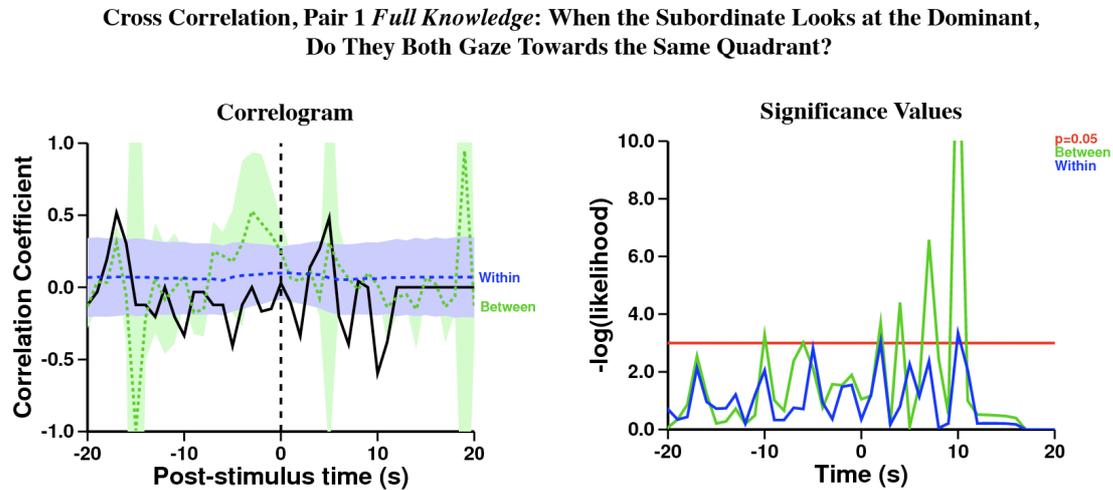


FIGURE 6.8: Referent behaviour: subordinate looking at dominant. Target behaviour: both chimpanzees gazing towards the same quadrant. After the subordinate looked at the dominant, the chimpanzees alternated between gazing and not gazing towards the same quadrant (peaks at time= +2, $r = -0.3380$, $n = 24$; $-\log\text{-likelihood} = 3.0236$, $p < 0.05$. time= +5, $r = 0.4804$, $n = 16$; $-\log\text{-likelihood} = 2.2633$, *ns*. time= +10, $r = -0.5976$, $n = 9$; $-\log\text{-likelihood} = 3.3408$, $p < 0.05$).

4. *No Bait, No Knowledge* controls

In the *No Bait, No Knowledge* controls, when the dominant looked at the subordinate, there was a trend in the data that both chimpanzees gazed towards the same quadrant; both chimpanzees also gazed towards the same quadrant 13 seconds later, and this relationship was only momentarily significant (Figure 6.9). This suggests that, in contrast to the sustained gaze reaction in the *Competition* trials, the dominant was not paying as close attention to the areas where the subordinate gazed in this condition.

Cross Correlation, Pair 1 *No Bait, No Knowledge*: When the Dominant Looks at the Subordinate, Do They Both Gaze Towards the Same Quadrant?

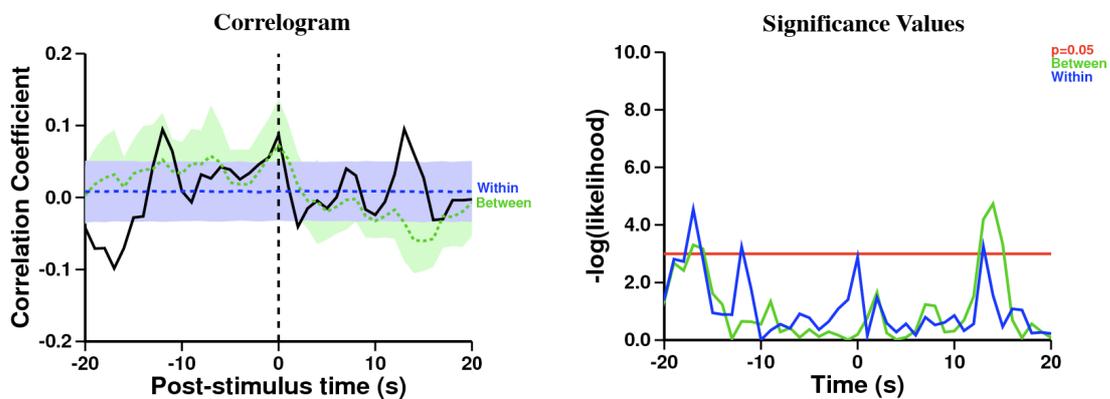


FIGURE 6.9: Referent behaviour: dominant looking at subordinate. Target behaviour: both chimpanzees gazing towards the same quadrant. At the moment that the dominant looked at the subordinate, both chimpanzees gazed towards the same quadrant; this relationship trends towards being more than expected from the within-trial shuffled control (peak at time= 0, $r=0.0872$, $n=593$; $-\log\text{-likelihood}=2.8815$, ns). The relationship is significantly more than expected many seconds later (peak at time= +13, $r=0.0950$, $n=597$; $-\log\text{-likelihood}=3.2573$, $p<0.05$).

Before the subordinate looked at the dominant, both chimpanzees were highly likely to be gazing towards the same quadrant when compared to the within-trial shuffled control (Figure 6.10). However, after the subordinate looked at the dominant, they did not gaze again towards the same quadrant until 13 seconds later, which is more likely to be a coincidence than an actual following relationship.

Cross Correlation, Pair 1 No Bait, No Knowledge: When the Subordinate Looks at the Dominant, Do They Both Gaze Towards the Same Quadrant?

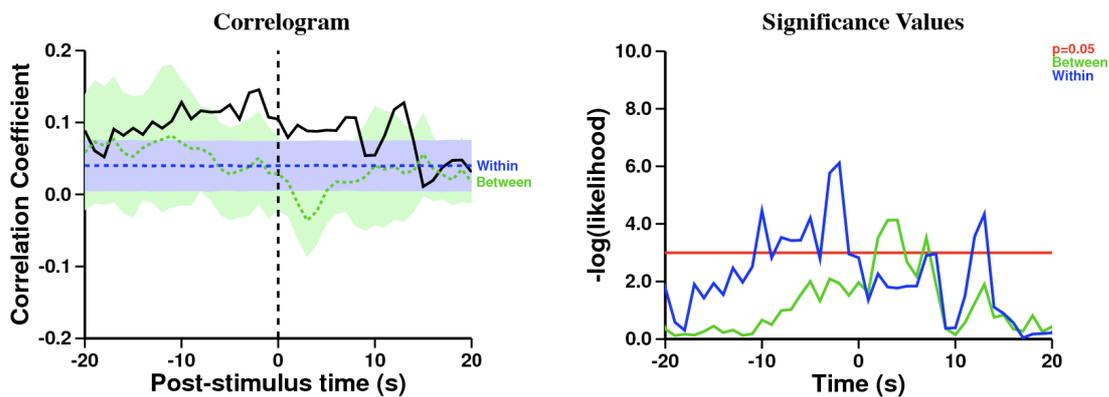


FIGURE 6.10: Referent behaviour: subordinate looking at dominant. Target behaviour: both chimpanzees gazing towards the same quadrant. Before the subordinate looked at the dominant, both chimpanzees were gazing towards the same quadrant (peak at time= -2, $r=0.1456$, $n=955$; $-\log\text{-likelihood}=6.1173$, $p<0.05$). Many seconds after the subordinate looked at the dominant, the chimpanzees were again gazing towards the same quadrant (peak at time= +13, $r=0.1275$, $n=927$; $-\log\text{-likelihood}=4.3429$, $p<0.05$).

5. Summary of *Static* Gaze Following behaviour

Throughout the *Competition*, the dominant followed the subordinate's *static* gaze, though the subordinate was unlikely to follow the dominant's *static* gaze. One possibility is that the dominant was more often physically following the subordinate's movement, which may have increased the likelihood that the dominant gazed towards the same location as the subordinate after looking at her. Since the gaze following data is consistent through all three phases, during which time the dominant used at least three very different movement following types, it is possible that the dominant used *static* gaze following as a tactic to gain information about the subordinate's direction of movement. While physical movement following can explain some of the trends in the data, it cannot explain the consistent opposite patterns of *static* gaze following between the two subjects in the *Competition*, since in some phases of the competition, the subordinate did follow the dominant's movement (see Chapter

5: Movement Following). An additional question of interest concerns whether the dominant followed the subordinate's gaze in an attempt to gain information about the location of the hidden food, because she may have been aware that the subordinate had seen where it was hidden.

The pattern of *static* gaze following was the opposite during the *Full Knowledge* controls: the subordinate followed the dominant's gaze, but the dominant did not follow the subordinate's. This may be due to the fact that the dominant ran out into the enclosure faster than the subordinate on two trials, so the dominant was physically in front of the subordinate, therefore reducing the likelihood that the dominant would look at the subordinate, and increasing the likelihood that the subordinate looked at the dominant, and towards the same quadrant as the dominant. Or, as Chance's (1967) social attention hypothesis would predict, the subordinate should look more often at the dominant than the reverse, though this is not supported by the data from the *Competition*. An additional explanation is that when the dominant had seen where the bait was hidden, she did not look to the subordinate for visual cues. In the *No Knowledge* and *No Bait, No Knowledge* controls, there are only trends towards *static* gaze following but the only significant result was that of both chimpanzees gazing towards the same quadrant after a delay of more than 10 seconds after the subordinate looked at the dominant in the *No Bait, No Knowledge* controls. However, this may not reflect a meaningful following relationship.

E. Following Gaze Onset

Here I present results of each subject following her opponent's gaze *onset*, which was defined as "one individual changes her gaze direction in view of the other, and then both chimpanzees gaze towards the same quadrant." I first address whether the dominant followed the subordinate's gaze *onset*, and then whether the subordinate followed the dominant's, for the entire *Competition* dataset (graphs showed consistent patterns across each of the three phases, so individual Phase graphs are included in the appendix to Chapter 6), then the *No Knowledge*, *Full Knowledge*, and *No Bait, No Knowledge* controls.

1. Entire *Competition* dataset

After the subordinate changed her gaze direction while in view of the dominant, both chimpanzees were significantly likely to gaze towards the same quadrant of their enclosure, indicating that the dominant matched the direction of the subordinate's gaze *onset* (Figure 6.11).

Cross Correlation, Pair 1 *Competition*: When the Subordinate Changes Gaze Direction in View of the Dominant, Do They Both Gaze Towards the Same Quadrant?

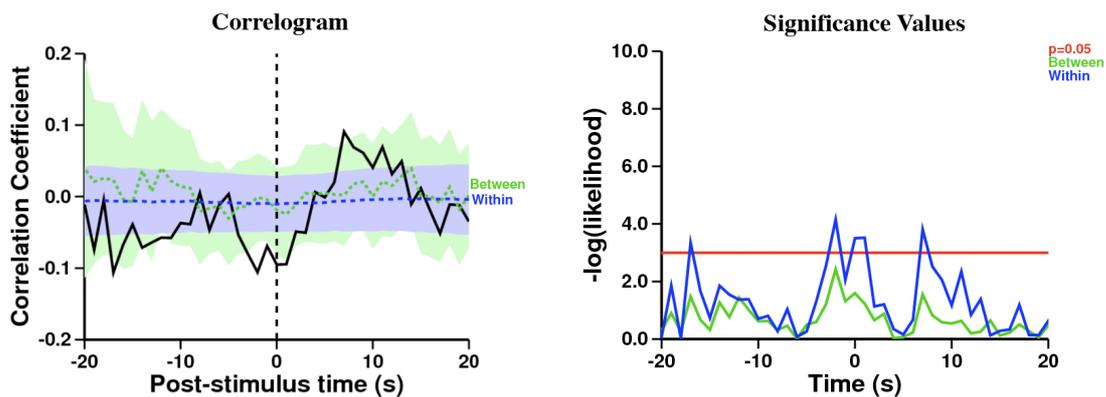


FIGURE 6.11: Referent behaviour: subordinate changes gaze direction in view of the dominant. Target behaviour: both chimpanzees gazing towards the same quadrant. Just before, and including the moment that the subordinate changed gaze direction, the chimpanzees were not gazing towards the same quadrant (peak at time= -2, $r = -0.1058$, $n = 733$; $-\log\text{-likelihood} = 4.1519$, $p < 0.05$), but several seconds later, both chimpanzees gazed together towards the same quadrant (peak at time= +7, $r = 0.0908$, $n = 592$; $-\log\text{-likelihood} = 3.8081$, $p < 0.05$).

Additionally, when the dominant changed her gaze direction while in view of the subordinate, the subordinate also gazed towards the same direction significantly more than expected four seconds later (Figure 6.12). In contrast to *static* gaze following, it appears that a visible change in the dominant's gaze direction did elicit the gaze following response in the subordinate.

Cross Correlation, Pair 1 *Competition*: When the Dominant Changes Gaze Direction in View of the Subordinate, Do They Both Gaze Towards the Same Quadrant?

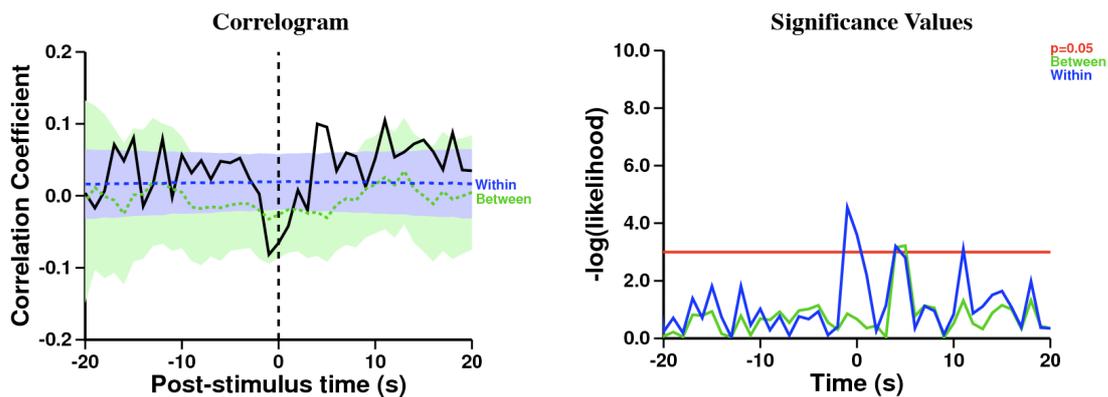


FIGURE 6.12: Referent behaviour: dominant changes gaze direction in view of the subordinate. Target behaviour: both chimpanzees gazing towards the same quadrant. Just before, and including the moment that the dominant changed gaze direction, the chimpanzees were not gazing towards the same quadrant (peak at time= -1, $r = -0.0817$, $n = 800$; $-\log$ -likelihood= 4.5520, $p < 0.05$), but a few seconds later, both chimpanzees gazed together towards the same quadrant (peak at time= +4, $r = 0.1000$, $n = 713$; $-\log$ -likelihood= 3.2011, $p < 0.05$).

2. No Knowledge controls

In the *No Knowledge* controls, there is no evidence that the dominant followed the subordinate's gaze onset (Figure 6.13).

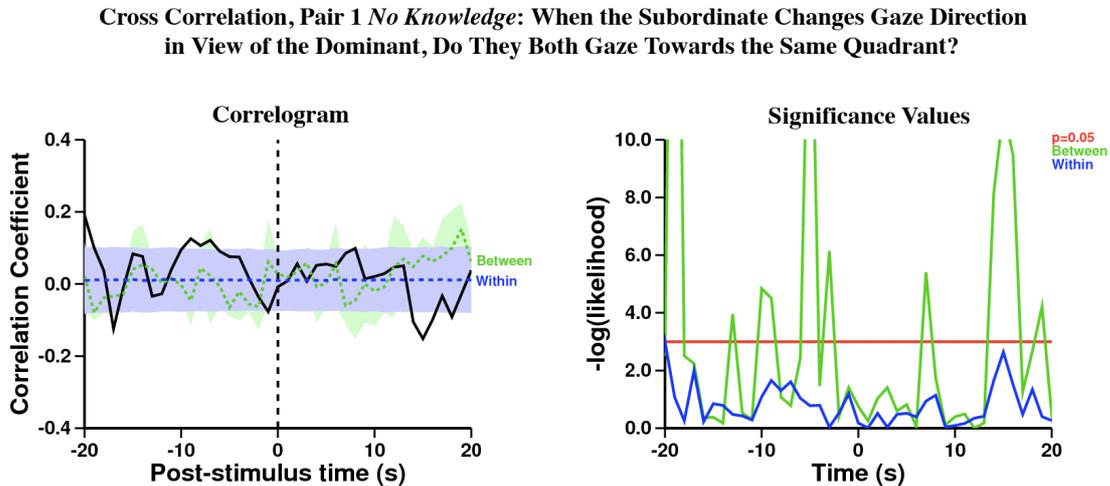


FIGURE 6.13: Referent behaviour: subordinate changes gaze direction in view of the dominant. Target behaviour: both chimpanzees gazing towards the same quadrant. There is no relationship between the two variables.

The subordinate followed the dominant's gaze onset in the *No Knowledge* control (Figure 6.14).

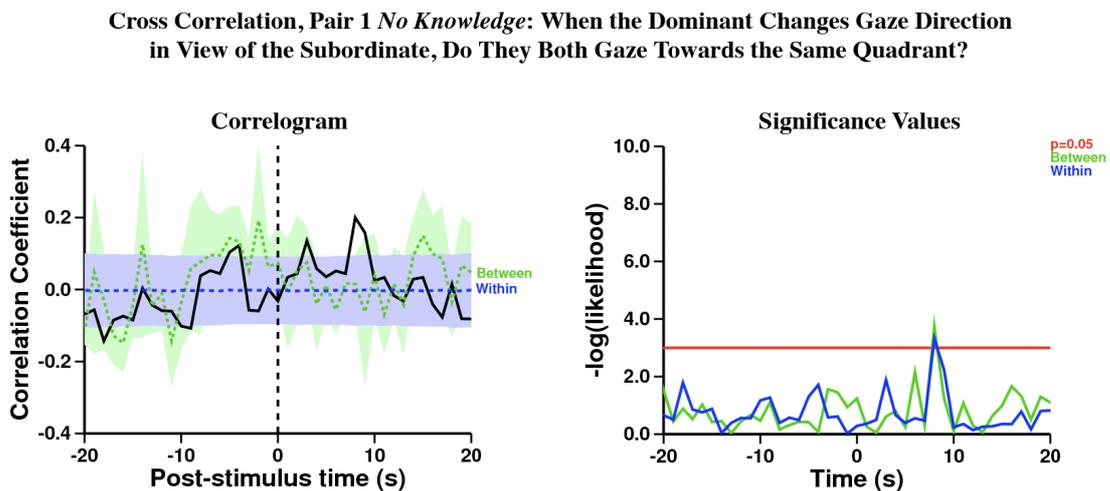


FIGURE 6.14: Referent behaviour: dominant changes gaze direction in view of the subordinate. Target behaviour: both chimpanzees gazing towards the same quadrant. Many seconds after the dominant changed gaze direction, both chimpanzees gazed towards the same quadrant significantly more than expected from the within-trial shuffled control (peak at time= +8, $r = 0.2002$, $n = 175$; $-\log\text{-likelihood} = 3.3176$, $p < 0.05$).

3. Full Knowledge controls

The dominant did not follow the subordinate's gaze *onset* in the *Full Knowledge* condition (Figure 6.15). As with *static* gaze, this can be explained by the fact that the dominant was physically in front of the subordinate on half of these trials, and inside the 'Cognition Room' on the other half of the trials, so there were few opportunities to follow gaze; furthermore, because the dominant had seen where the food was hidden, she did not need to look to the subordinate for any visual cue.

Cross Correlation, Pair 1 *Full Knowledge*: When the Subordinate Changes Gaze Direction in View of the Dominant, Do They Both Gaze Towards the Same Quadrant?

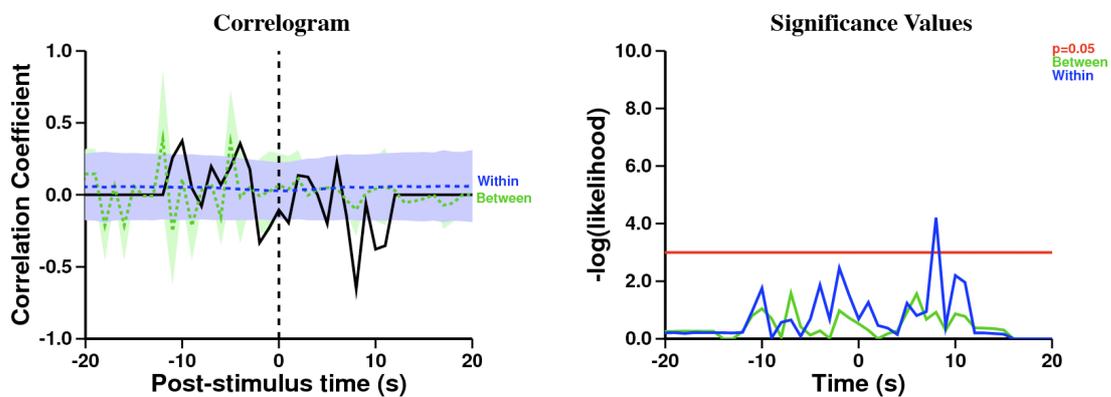


FIGURE 6.15: Referent behaviour: subordinate changes gaze direction in view of the dominant. Target behaviour: both chimpanzees gazing towards the same quadrant. Several seconds after the subordinate changed gaze direction, both chimpanzees gazed towards the same quadrant significantly less than expected from the within-trial shuffled control (peak at time= +8, $r = -0.6547$, $n = 10$; $-\log\text{-likelihood} = 4.2102$, $p < 0.05$)

Though the relationship is not significant, the pattern in the correlogram shows that the subordinate did follow the dominant's gaze *onset* in the *Full Knowledge* controls (Figure 6.16). Again this is likely to be an effect of the dominant running ahead of the subordinate. However, it is clear that the graph is skewed due to low sample size: when the dominant ran towards the bait (2 trials), she did not change her gaze direction often, and on the remaining two trials, the dominant stayed inside so the dominant's gaze was not recorded, and the subordinate was unlikely to witness it.

Cross Correlation, Pair 1 *Full Knowledge*: When the Dominant Changes Gaze Direction in View of the Subordinate, Do They Both Gaze Towards the Same Quadrant?

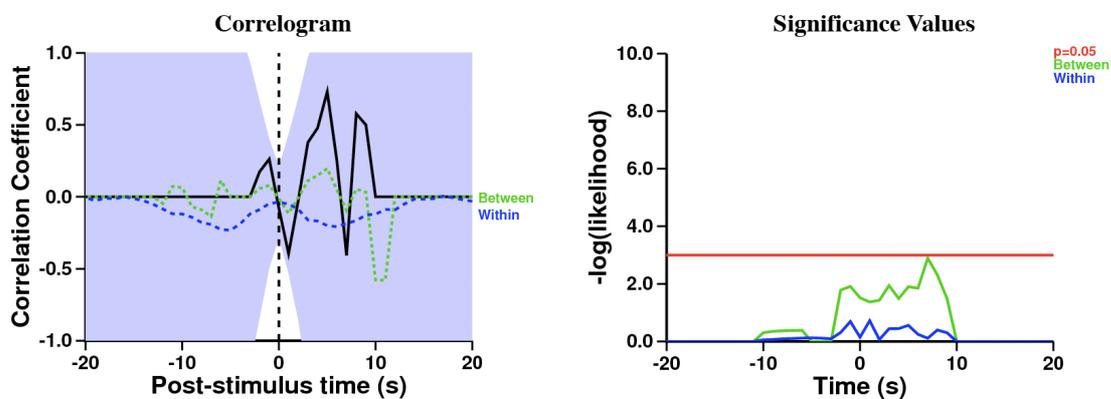


FIGURE 6.16: Referent behaviour: dominant changes gaze direction in view of the subordinate. Target behaviour: both chimpanzees gazing towards the same quadrant. After the dominant changed her gaze direction, the pattern in the correlogram shows that both chimpanzees gazed towards the same quadrant, but this relationship is not significant.

4. No Bait, No Knowledge controls

Though there was no hidden food (and therefore no information relevant to the experiment to be gained through either movement or gaze following), both subjects did follow their competitor's gaze *onset* in the *No Bait, No Knowledge* controls (Figures 6.17 and 6.18).

Cross Correlation, Pair 1 *No Bait, No Knowledge*: When the Subordinate Changes Gaze Direction in View of the Dominant, Do They Both Gaze Towards the Same Quadrant?

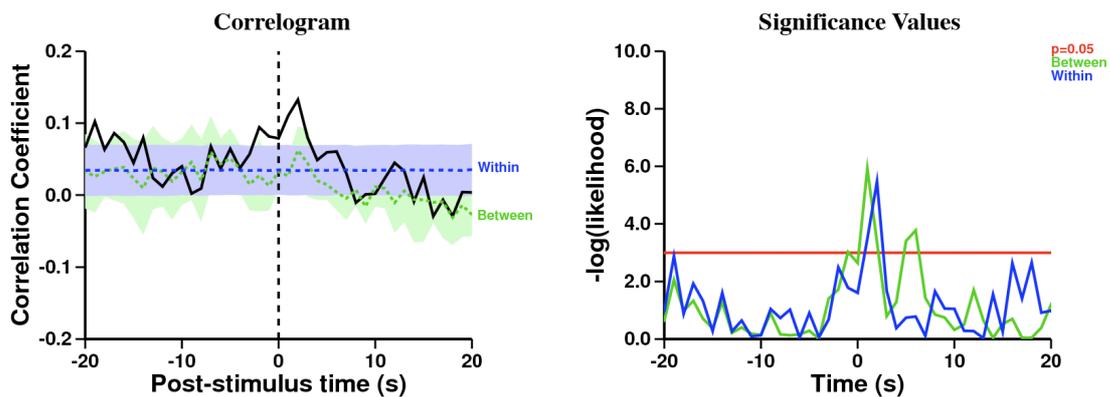


FIGURE 6.17: Referent behaviour: subordinate changes gaze direction in view of the dominant. Target behaviour: both chimpanzees gazing towards the same quadrant. After the subordinate changed her gaze direction, both chimpanzees gazed towards the same quadrant (peak at time= +2, $r = 0.1327$, $n = 986$; $-\log\text{-likelihood} = 5.4719$, $p < 0.05$).

Cross Correlation, Pair 1 *No Bait, No Knowledge*: When the Dominant Changes Gaze Direction in View of the Subordinate, Do They Both Gaze Towards the Same Quadrant?

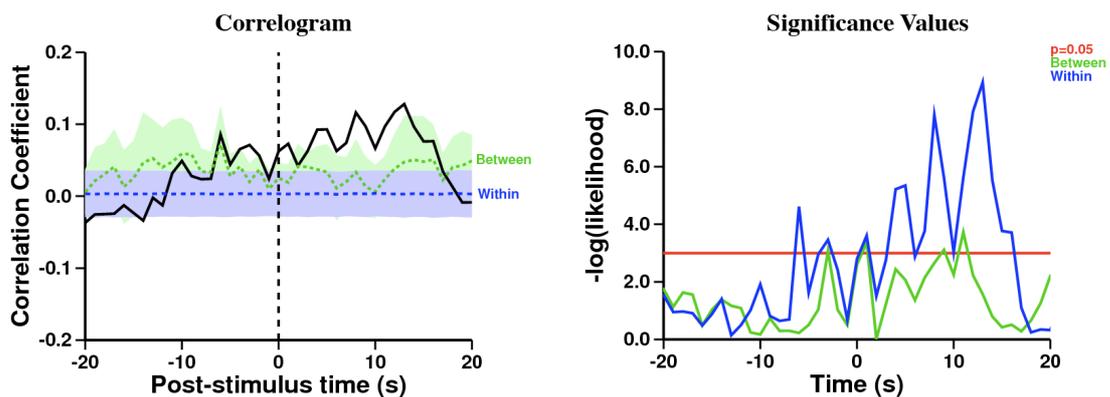


FIGURE 6.18: Referent behaviour: dominant changes gaze direction in view of the subordinate. Target behaviour: both chimpanzees gazing towards the same quadrant. Both before and after the dominant changed her gaze direction, both chimpanzees were significantly likely to be gazing towards the same quadrant (peak at time= +13, $r = 0.1280$, $n = 975$; $-\log\text{-likelihood} = 8.9300$, $p < 0.05$).

5. Summary of Following Gaze *Onset* behaviour

Throughout the experiment and all the control conditions, the subordinate followed the dominant's gaze *onset*, which suggests that a visible change in the dominant's gaze direction was a salient cue that affected the subordinate's subsequent gaze behaviour. The dominant only followed the subordinate's gaze change significantly more than expected in the *Competition* trials and the *No Bait, No Knowledge* trials, but not in the *Full Knowledge* or *No Knowledge* controls.

The dominant clearly paid more attention to the subordinate's gaze direction: whereas the dominant followed both the subordinate's *static* and dynamic gaze *onset*, the subordinate only seemed to notice when the dominant changed her direction of gaze.

F. How Gaze Following Relates to Movement Following

This section addresses how patterns of gaze following relate to the different movement following patterns of each subject: *approach*; *footsteps*; and *converge*. I will address questions such as, does gaze following lead to movement following, or does movement following influence gaze following? Does incongruent gaze precede a change of movement direction? And can gaze cues be withheld?

1. *Approach*

Following by *approaching*, or walking towards the opponent from a different quadrant, required the dominant to constantly re-adjust her movement in response to the subordinate's movement (in the case that the subordinate was moving). To determine the relationship between this type of movement following and gaze following, I asked, "When the dominant *approaches* the subordinate, does the dominant follow the subordinate's *static* gaze?" The dominant followed the subordinate's *static* gaze before she *approached* the subordinate, and continued to follow the subordinate's *static* gaze for several seconds as she *approached* (Figure 6.19).

**Cross Correlation, Pair 1 *Competition*: When the Dominant *Approaches* the Subordinate,
Does the Dominant Follow the Subordinate's *Static* Gaze?**

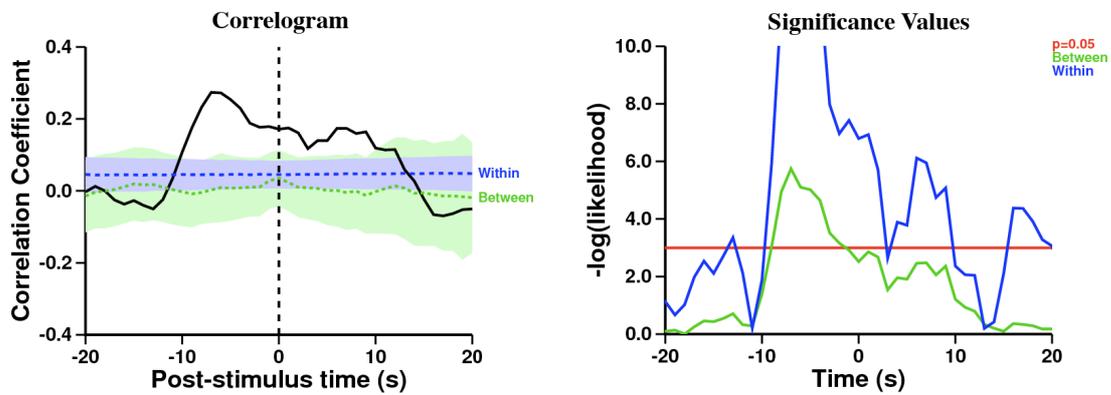


FIGURE 6.19: Referent behaviour: dominant *approaching* the subordinate. Target behaviour: dominant follows the subordinate's *static* gaze. Both before and after the dominant walked towards the subordinate from a different quadrant, she was significantly likely to look at the subordinate and then both chimpanzees gazed towards the same quadrant (peak at time= -6, $r= 0.2723$, $n= 683$; $-\log\text{-likelihood}= 17.0444$, $p<0.05$. Peak at time= +6, $r= 0.1734$, $n= 699$; $-\log\text{-likelihood}= 6.1173$, $p<0.05$).

When the chimpanzees were in different quadrants, the dominant nearly immediately walked towards the subordinate, though overall it took several seconds longer for the subordinate to walk towards the dominant (see Chapter 5: Movement Following). When the subordinate did *approach* the dominant, she also followed her *static* gaze (Figure 6.20). However, unlike the dominant, the subordinate's gaze following reaction was not sustained.

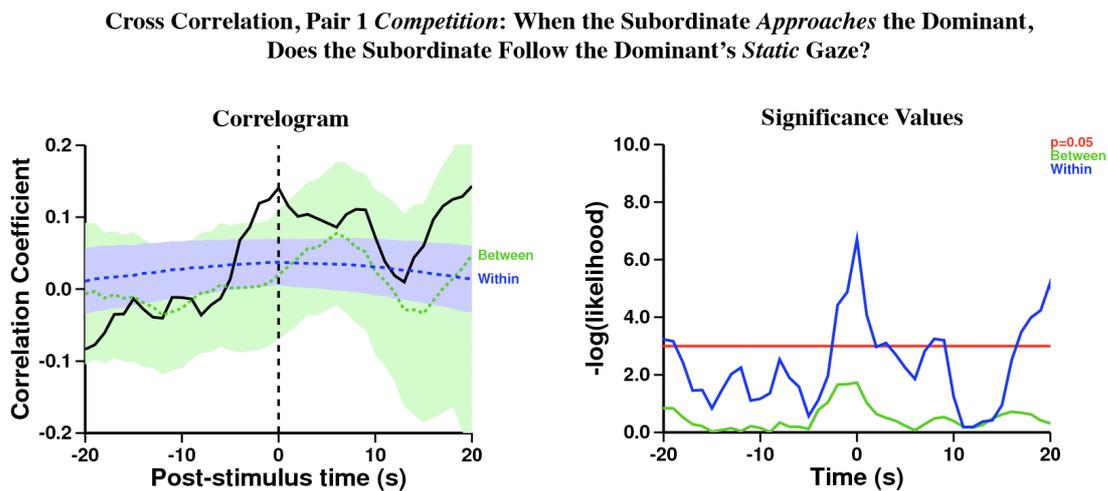


FIGURE 6.20: Referent behaviour: subordinate *approaching* the dominant. Target behaviour: subordinate following the dominant's *static* gaze. At the moment that the subordinate walked towards the dominant from a different quadrant, she looked at the dominant and then both chimpanzees gazed towards the same quadrant (peak at time= 0, $r=0.1403$, $n=820$; $-\log(\text{likelihood})=6.7107$, $p<0.05$).

Whereas both subjects followed the other's *static* gaze while *approaching*, following gaze *onset* was not as positively correlated with *approach* behaviour. In fact, when the dominant *approached* the subordinate, she was significantly unlikely to follow a change in the subordinate's gaze direction (Figure 6.21). There was no relation of the subordinate following the dominant's gaze *onset* after she *approached* the dominant (Figure 6.22).

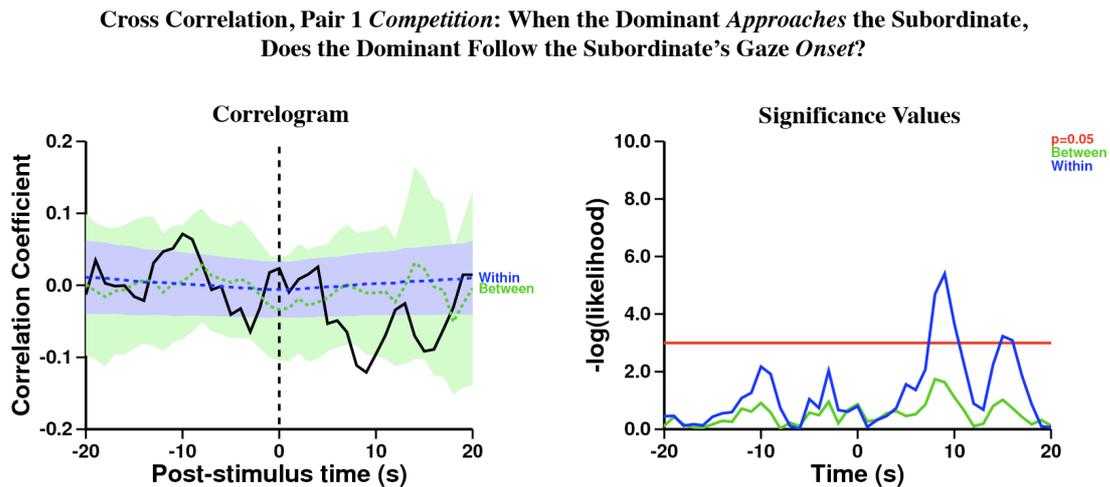


FIGURE 6.21: Referent behaviour: dominant *approaching* the subordinate. Target behaviour: dominant following the subordinate's gaze *onset*. After the dominant walked towards the subordinate from a different quadrant, the subordinate changed her gaze direction in view of the dominant and then both chimpanzees gazed towards the same quadrant significantly less than expected from the within-trial shuffled control (peak at time= +9, $r = -0.1210$, $n = 558$; $-\log\text{-likelihood} = 5.4008$, $p < 0.05$).

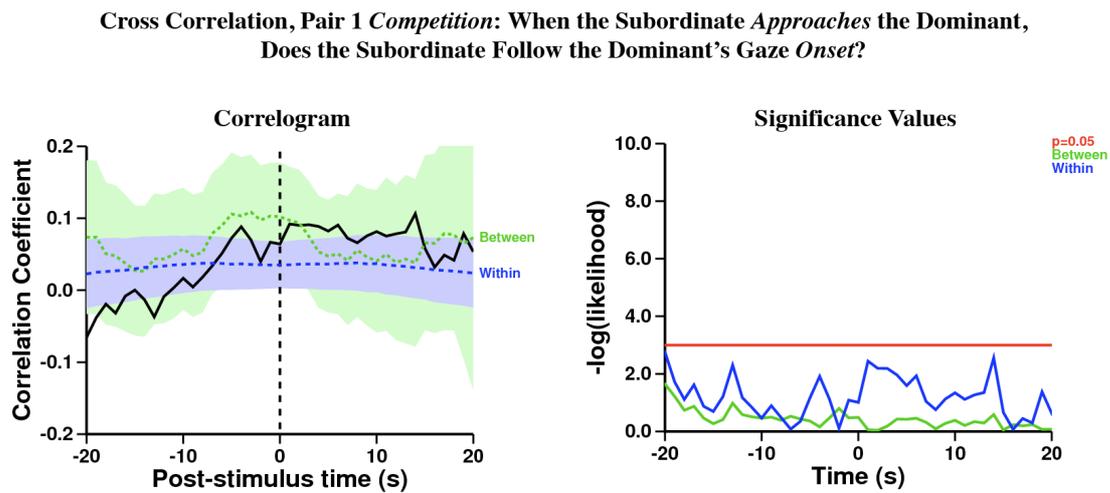


FIGURE 6.22: Referent behaviour: subordinate *approaching* the dominant. Target behaviour: subordinate following the dominant's gaze *onset*. After the subordinate walked towards the dominant from a different quadrant, the dominant changed her gaze in view of the subordinate and then both chimpanzees gazed towards the same quadrant; this relationship trends towards being more than expected from the within-trial shuffled control (peak at time= +1, $r = 0.0920$, $n = 788$; $-\log\text{-likelihood} = 2.4406$, *ns*. Time= +14, $r = 0.1063$, $n = 513$; $-\log\text{-likelihood} = 2.5534$, *ns*).

Both subjects followed their opponent's *static* gaze when they *approached*, but they did not follow the other's gaze *onset*. Perhaps because the chimpanzees were in two different quadrants, one subject's quick change in gaze direction was less noticeable to her approaching opponent than the subject's steady gaze in one direction.

The dominant's *approach* tactic caused the subordinate to stop walking towards the bait especially during Phase 3 of the *Competition* (see Chapter 5: Movement Following). When the subordinate stopped walking, it functioned to withhold information from the dominant about the location of the hidden bait. Furthermore, after the subordinate stopped walking for five seconds, she also stopped gazing towards the bait (Figure 6.23, "Stop Gazing" was defined as a change from "Gazing towards the bait" to five consecutive seconds of "Not gazing towards the bait"). The dominant appeared to follow the subordinate's *static* gaze before *approaching* (i.e., her gaze informed her movement); the subordinate's tactic of not gazing towards the bait may have prevented the dominant from following her gaze and then moving towards where the bait was hidden. The subordinate was not only capable of withholding her desire to retrieve the food, but also capable of preventing the dominant from gaining further visual information by following the subordinate's gaze towards the bait.

**Cross Correlation, Pair 1 Competition: When the Subordinate Stops Walking,
Does she Stop Gazing Towards the Bait?**

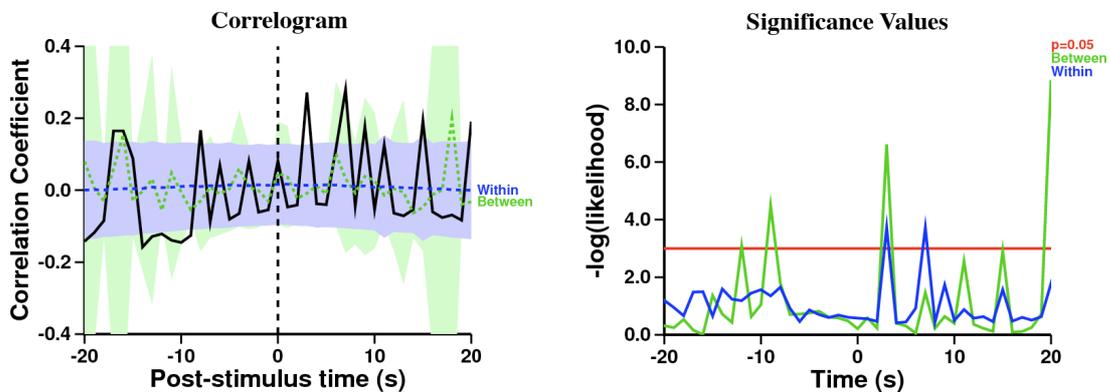


FIGURE 6.23: Referent behaviour: subordinate stops walking. Target behaviour: subordinate stops gazing towards the bait. After the subordinate stopped walking for five seconds, she stopped gazing towards the bait for five seconds (peak at time= +3, $r = 0.2715$, $n = 153$; $-\log\text{-likelihood} = 3.7301$, $p < 0.05$. Time= +7, $r = 0.2796$, $n = 119$; $-\log\text{-likelihood} = 3.7243$, $p < 0.05$).

2. Footsteps

Following in the other's *footsteps* (i.e., when both chimpanzees are in the same quadrant and walking towards the same quadrant, and one individual is walking towards the other and the other walking away from the first individual) may present a unique opportunity for the follower to closely monitor the leader's gaze. Several seconds before the dominant followed in the subordinate's *footsteps*, she followed the subordinate's *static* gaze (Figure 6.24). However, once she was in the subordinate's *footsteps*, the correlation coefficient of *static* gaze following only trended towards being more than expected from the within-trial shuffled control. The pattern in the correlogram shows that the dominant momentarily followed the subordinate's *static* gaze but then was unlikely to do so.

Cross Correlation, Pair 1 Competition: When the Dominant Follows in the Subordinate's *Footsteps*, Does the Dominant Follow the Subordinate's *Static* Gaze?

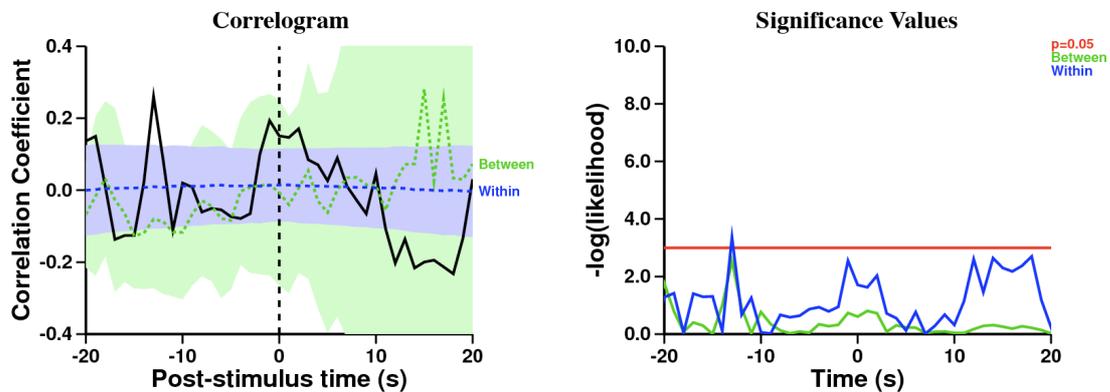


FIGURE 6.24: Referent behaviour: dominant following in the subordinate's *footsteps*. Target behaviour: dominant following the subordinate's *static* gaze. Before the dominant was in the same quadrant and walking towards the same quadrant as the subordinate (and the dominant walking towards the subordinate and the subordinate away from the dominant), the dominant looked at the subordinate and then both chimps gazed towards the same quadrant; this relationship trends towards being more than expected from the within-trial shuffled control (peak at time= -1, $r = 0.1936$, $n = 114$; $-\log\text{-likelihood} = 2.5498$, *ns*). Many seconds later, this relationship trends towards being less than expected from the within-trial shuffled control (peak at time= +18, $r = -0.2326$, $n = 53$; $-\log\text{-likelihood} = 2.6979$, *ns*). The dominant followed the subordinate's *static* gaze before following in her *footsteps* (peak at time= -13, $r = 0.2605$, $n = 80$; $-\log\text{-likelihood} = 3.3669$, $p < 0.05$).

Though for the overall *Competition* dataset the subordinate did not follow the dominant's *static* gaze, one situation in which she did follow the dominant's gaze was when she was walking directly behind her, in her *footsteps* (Figure 6.25), possibly due to the natural attention structure described by Chance (1967): the subordinate should look to the dominant, and to where the dominant is looking.

Cross Correlation, Pair 1 *Competition*: When the Subordinate Follows in the Dominant's *Footsteps*, Does the Subordinate Follow the Dominant's *Static* Gaze?

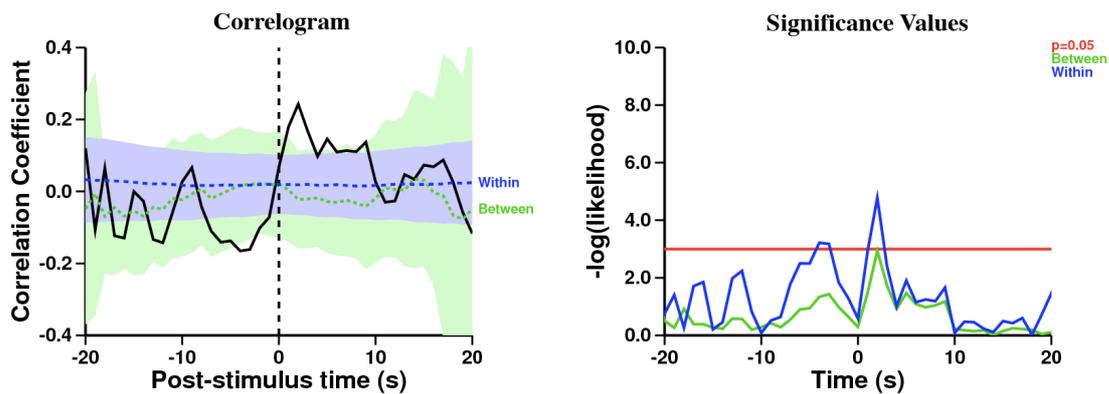


FIGURE 6.25: Referent behaviour: subordinate following in the dominant's *footsteps*. Target behaviour: subordinate following the dominant's *static* gaze. After the subordinate was in the same quadrant and walking towards the same quadrant as the dominant (and the subordinate walking towards the dominant and the dominant away from the subordinate), the subordinate looked at the dominant and then both chimpanzees gazed towards the same quadrant (peak at time= +2, $r = 0.2427$, $n = 176$; $-\log\text{-likelihood} = 4.7826$, $p < 0.05$). Before the subordinate followed in the dominant's *footsteps*, she was significantly unlikely to follow the dominant's *static* gaze (peak at time= -4, $r = -0.1655$, $n = 114$; $-\log\text{-likelihood} = 3.2182$, $p < 0.05$).

The dominant followed the subordinate's gaze *onset* while following in her *footsteps* (Figure 6.26). Perhaps due to closer proximity (this is the only movement definition for which the chimpanzees were both in the same quadrant), the dominant was able to utilize the gaze *onset* cue, which may have gone unnoticed at greater distances.

Cross Correlation, Pair 1 Competition: When the Dominant Follows in the Subordinate's Footsteps, Does the Dominant Follow the Subordinate's Gaze Onset?

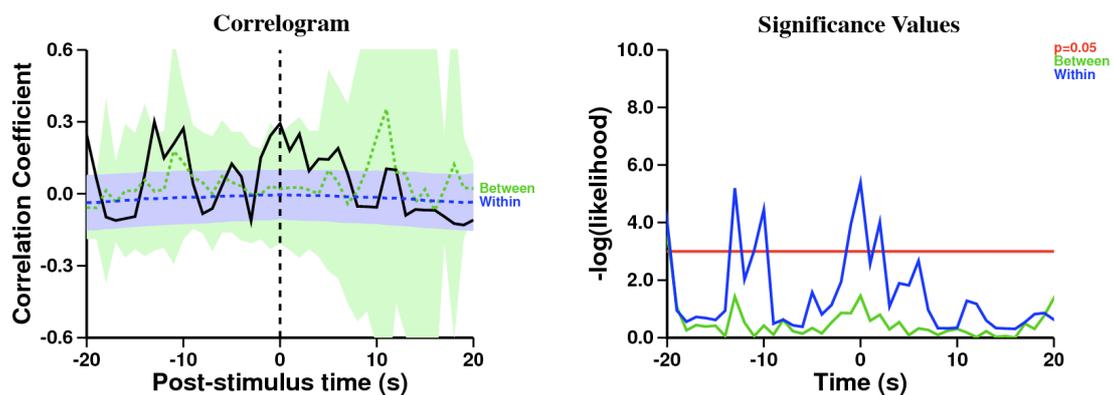


FIGURE 6.26: Referent behaviour: dominant following in the subordinate's *footsteps*. Target behaviour: dominant following the subordinate's gaze *onset*. At the moment that the dominant was in the same quadrant and walking towards the same quadrant as the subordinate (and the dominant walking towards the subordinate and the subordinate away from the dominant), the subordinate changed her gaze direction in view of the dominant and then both chimpanzees gazed towards the same quadrant (peak at time= 0, $r = 0.2931$, $n = 111$; $-\log\text{-likelihood} = 5.3873$, $p < 0.05$). The dominant also followed the subordinate's gaze *onset* before she followed in the subordinate's *footsteps* (peak at time= -13, $r = 0.3002$, $n = 74$; $-\log\text{-likelihood} = 5.1960$, $p < 0.05$).

When the subordinate followed in the dominant's *footsteps*, she followed the dominant's gaze *onset* (Figure 6.27).

Cross Correlation, Pair 1 *Competition*: When the Subordinate Follows in the Dominant's *Footsteps*, Does the Subordinate Follow the Dominant's Gaze *Onset*?

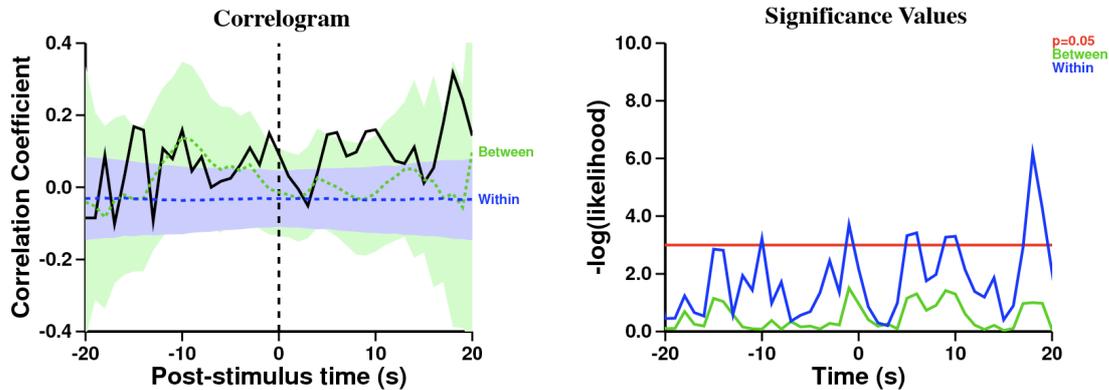


FIGURE 6.27: Referent behaviour: subordinate following in the dominant's *footsteps*. Target behaviour: subordinate following the dominant's gaze *onset*. Before, and soon after the subordinate was in the same quadrant and walking towards the same quadrant as the dominant (and the subordinate walking towards the dominant and the dominant away from the subordinate), the dominant changed her gaze direction in view of the subordinate and then both chimpanzees gazed towards the same quadrant (peak at time= -1, $r = 0.1498$, $n = 158$; $-\log\text{-likelihood} = 3.7100$, $p < 0.05$. Peak at time= + 6, $r = 0.1522$, $n = 152$; $-\log\text{-likelihood} = 3.4206$, $p < 0.05$). The subordinate also followed the dominant's gaze *onset* before she followed in the dominant's *footsteps* (peak at time= -10, $r = 0.1588$, $n = 80$; $-\log\text{-likelihood} = 3.2216$, $p < 0.05$).

Both subjects followed their opponent's *static gaze*, as well as their gaze *onset*, when they were physically following in the other's *footsteps*. It is an obvious artefact, rather than an independent effect, that following in the other's footsteps would result in *static gaze* following: in the case that both chimpanzees are looking straight ahead towards the same quadrant, the follower simultaneously looks at the leader as well as the quadrant directly in front of both of them (i.e., the definition of *static gaze* following). Close proximity may also make the gaze *onset* cue more noticeable to the follower.

3. Incongruent Gaze and Body Direction

It is notable that the subject in the follower position reacted to the leader's gaze change by also gazing towards the same quadrant: it may be a salient cue preceding a change in movement direction (Nummenmaa et al., 2009). To test this hypothesis, I asked, "When the subordinate's gaze and body direction are incongruent (i.e., towards different quadrants), does the subordinate change her body direction?" When the subordinate walked towards one quadrant but gazed towards another, she was significantly likely to change the direction of her body six seconds later (Figure 6.28).

Cross Correlation, Pair 1 *Competition*: When the Subordinate's Gaze and Body Direction are Incongruent, Does the Subordinate Change Body Direction?

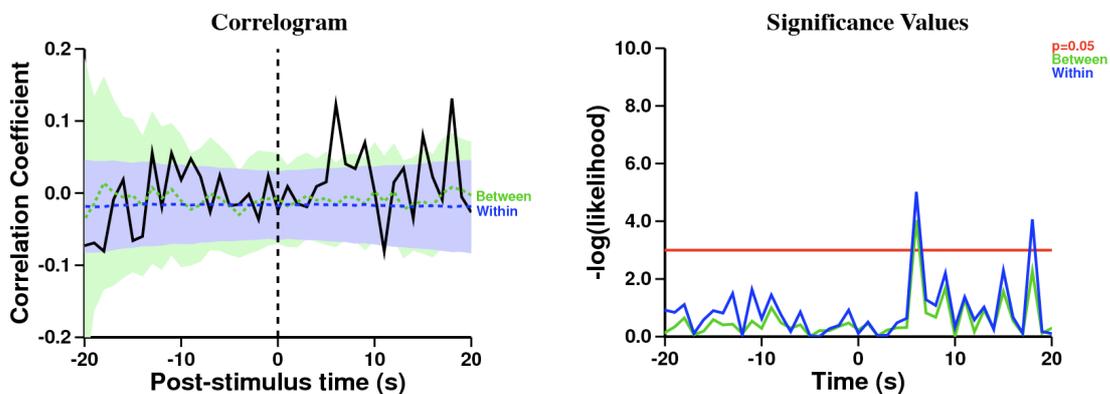


FIGURE 6.28: Referent behaviour: the subordinate's gaze and body direction are incongruent. Target behaviour: subordinate changing her body direction. After the subordinate walked towards one quadrant while gazing towards another, she changed her body direction (peak at time= +6, $r= 0.1229$, $n= 407$; $-\log\text{-likelihood}= 5.0175$, $p<0.05$).

Furthermore, when the subordinate's gaze and body direction were incongruent, the dominant did follow her gaze *onset* (Figure 6.29), indicating that if the subordinate were to change her gaze direction towards the food before changing her body direction, she might betray its location to the dominant.

Cross Correlation, Pair 1 Competition: When the Subordinate's Gaze and Body Direction are Incongruent, Does the Dominant Follow the Subordinate's Gaze Onset?

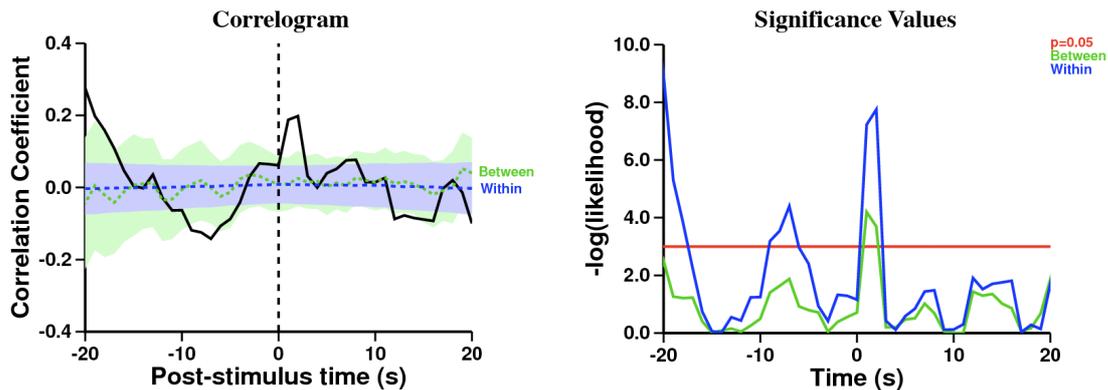


FIGURE 6.29: Referent behaviour: the subordinate's gaze and body direction are incongruent. Target behaviour: dominant follows the subordinate's gaze *onset*. After the subordinate walked towards one quadrant while gazing towards another, the dominant was significantly likely to follow the subordinate's change in gaze direction (peak at time= +2, $r=0.1980$, $n=447$; $-\log\text{-likelihood}=7.7512$, $p<0.05$).

Similar to the subordinate, the dominant's incongruent gaze and body direction preceded a change in body direction significantly more than expected (Figure 6.30).

Cross Correlation, Pair 1 Competition: When the Dominant's Gaze and Body Direction are Incongruent, Does the Dominant Change Body Direction?

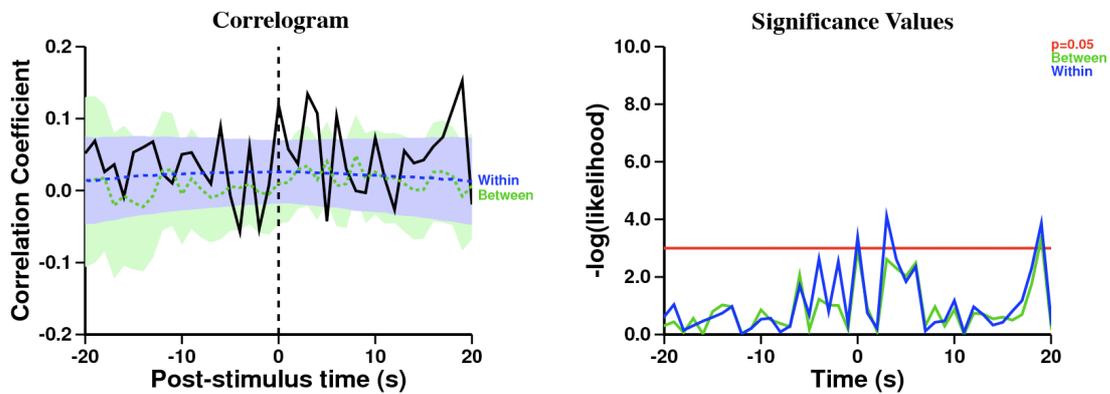


Figure 6.30: Referent behaviour: dominant's gaze and body direction are incongruent. Target behaviour: dominant changing her body direction. After the dominant walked towards one quadrant while gazing towards another, she changed her body direction (peak at time= +3, $r = 0.1342$, $n = 471$; $-\log\text{-likelihood} = 4.1100$, $p < 0.05$).

Furthermore, when the dominant's gaze and body direction were incongruent, the subordinate followed the dominant's gaze onset (Figure 6.31).

Cross Correlation, Pair 1 Competition: When the Dominant's Gaze and Body Direction are Incongruent, Does the Subordinate Follow the Dominant's Gaze Onset?

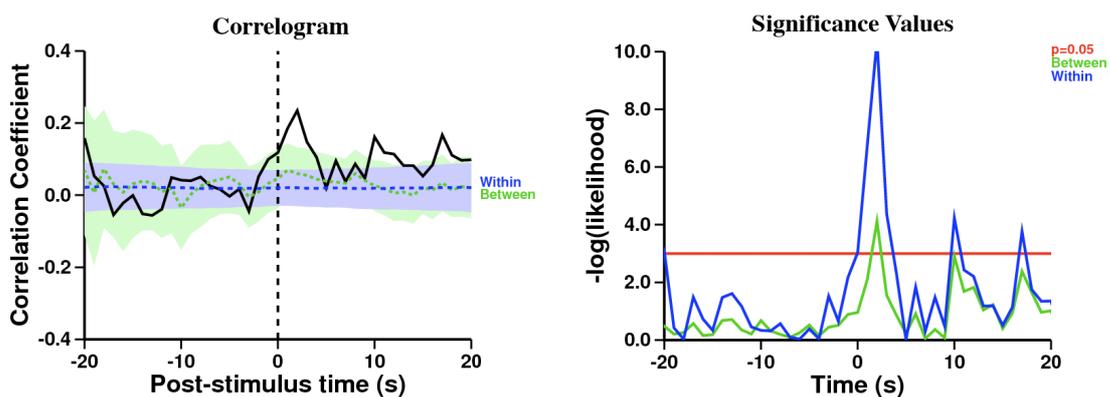


FIGURE 6.31: Referent behaviour: dominant's gaze and body direction are incongruent. Target behaviour: subordinate follows the dominant's gaze onset. After the dominant walked towards one quadrant while gazing towards another, the subordinate was significantly likely to follow the dominant's change in gaze direction (peak at time= +2, $r = 0.2347$, $n = 355$; $-\log\text{-likelihood} = 10.3987$, $p < 0.05$).

For each subject, incongruent gaze and body direction preceded a change in her direction of movement. When one chimpanzee had incongruent gaze and body direction, the other subject was highly likely to notice and follow that chimpanzee's change in gaze direction.

4. Convergence

When the chimpanzees *converged* (i.e., in different quadrants and walking towards the same quadrant), only the dominant followed the subordinate's *static* gaze, but the subordinate did not follow the dominant's (Figures 6.32 and 6.33). While I cannot determine upon which subject's movement her opponent's movement is contingent in *converging* behaviour (due to the inclusive definition), the *static* gaze following results lend support to the interpretation that the dominant is extrapolating the subordinate's movement, and not the other way around.

Cross Correlation, Pair 1 *Competition*: When Both Chimpanzees Converge, Does the Dominant Follow the Subordinate's *Static* Gaze?

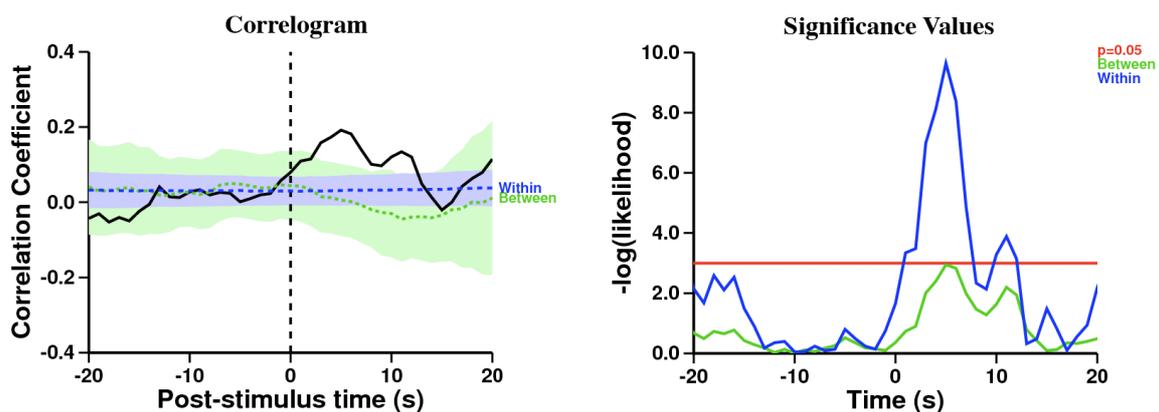


FIGURE 6.32: Referent behaviour: both chimpanzees *converging*. Target behaviour: dominant following the subordinate's *static* gaze. After both chimpanzees were in different quadrants and moving towards the same quadrant, the dominant looked at the subordinate and then both chimpanzees gazed towards the same quadrant significantly more than expected from the within-trial shuffled control (Peak at time= +5, $r = 0.1917$, $n = 722$; $-\log\text{-likelihood} = 9.6411$, $p < 0.05$).

**Cross Correlation, Pair 1 Competition: When Both Chimpanzees Converge,
Does the Subordinate Follow the Dominant's Static Gaze?**

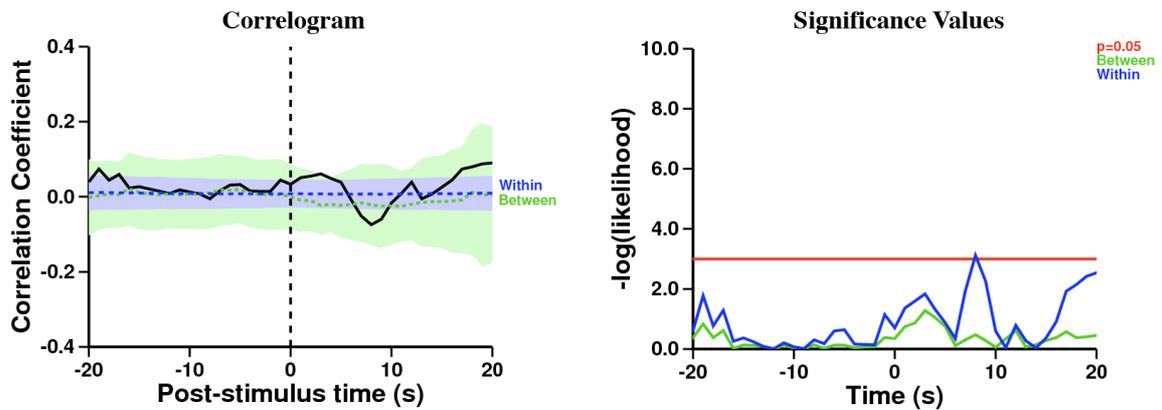


FIGURE 6.33: Referent behaviour: both chimpanzees *converging*. Target behaviour: subordinate following the dominant's *static* gaze. After both chimpanzees were in different quadrants and moving towards the same quadrant, the subordinate looked at the dominant and then both chimpanzees gazed towards the same quadrant significantly less than expected from the within-trial shuffled control (Peak at time= +8, $r = -0.0744$, $n = 657$; $-\log\text{-likelihood} = 3.1160$, $p < 0.05$).

When both chimpanzees were in different quadrants and walking towards the same quadrant, both the dominant and the subordinate were significantly unlikely to follow their opponent's gaze *onset* (Figures 6.34 and 6.35).

**Cross Correlation, Pair 1 *Competition*: When Both Chimpanzees Converge,
Does the Dominant Follow the Subordinate's Gaze Onset?**

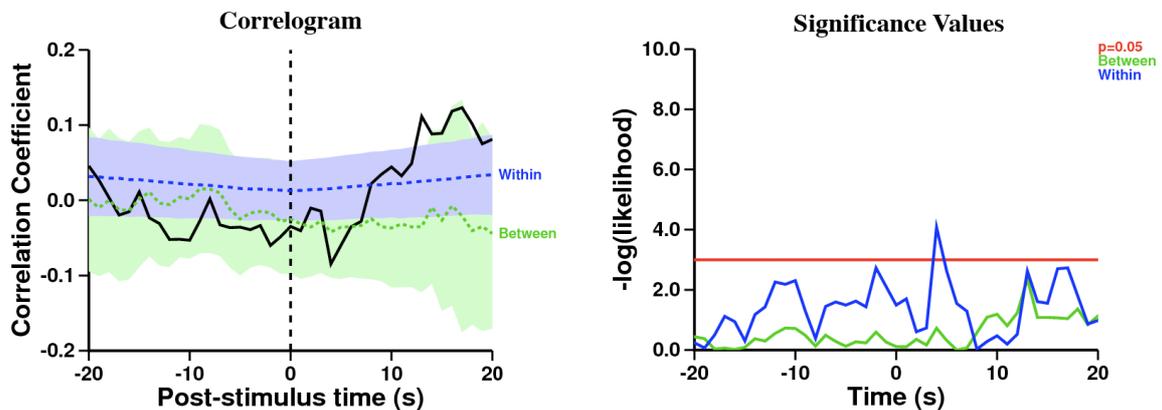


FIGURE 6.34: Referent behaviour: both chimpanzees *converging*. Target behaviour: dominant following the subordinate's gaze *onset*. After both chimpanzees were in different quadrants and walking towards the same quadrant, the subordinate changed her gaze direction in view of the dominant and then both chimpanzees gazed towards the same quadrant significantly less than expected from the within-trial shuffled control (peak at time= +4, $r = -0.0846$, $n = 673$; $-\log\text{-likelihood} = 4.0801$, $p < 0.05$). A few seconds later, this relationship trends towards being more than expected from the within-trial shuffled control (peak at time= +17, $r = 0.1231$, $n = 414$; $-\log\text{-likelihood} = 2.7291$, *ns*).

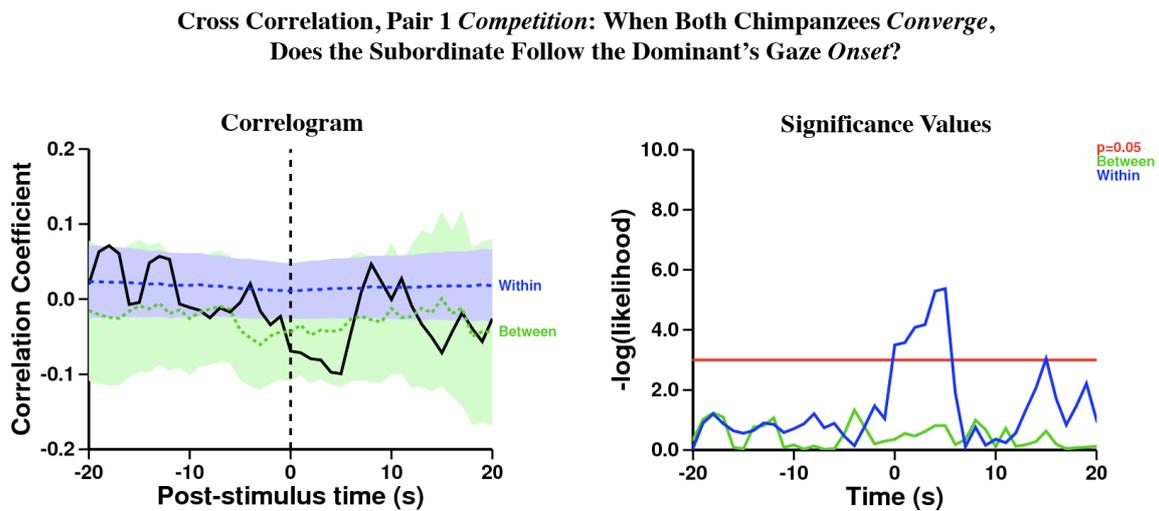


FIGURE 6.35: Referent behaviour: both chimpanzees *converging*. Target behaviour: subordinate following the dominant's gaze *onset*. After the chimpanzees were in different quadrants and walking towards the same quadrant, the dominant changed her gaze direction in view of the subordinate and then both chimpanzees gazed towards the same quadrant significantly less than expected from the within-trial shuffled control (peak at time= +5, $r = -0.0715$, $n = 690$; $-\log\text{-likelihood} = 5.3720$, $p < 0.05$).

After the chimpanzees started *converging*, the dominant followed the subordinate's *static* gaze, perhaps indicating that the dominant was using the subordinate's gaze cue to determine the direction that the subordinate was headed, in order to modify her own movement to end up at the same location with the subordinate.

5. Summary

The dominant followed the subordinate's *static* gaze when she used the three defined movement types, which suggests that when she physically followed she also gained visual information through gaze following. The subordinate overall physically followed the dominant less, but on the occasions that she *approached* and followed in the dominant's *footsteps*, the subordinate followed the dominant's *static* gaze, which could indicate that gaze following is more likely while also physically following. However, the subordinate did not follow the dominant's *static* gaze when both chimpanzees *converged*. Results show that *static* gaze following coincided temporarily with movement following: gaze follows occurred at the moment or shortly after a movement follow was initiated, which implies that a gaze follow did not lead to a movement follow, but rather that physically following the other chimpanzee led to an increase in the *static* gaze following response of the follower.

Though in the overall *Competition* dataset both subjects noticed the other's gaze *onset*, this was not positively correlated with either the *approach* or the *converge* movement types. Both the dominant and the subordinate followed the other's gaze *onset* when in close proximity and following in the other's *footsteps*. It may be that changes in gaze direction are more noticeable at short distances than *static* gaze, and that changes are especially salient when following in the other's footsteps as changes in gaze direction precede changes in movement direction (Nummenmaa et al., 2009).

IV. Overall Summary of Pair 1, Missy and Rita

I examined two types of gaze behaviour: *static* gaze following and following gaze *onset* (Table 6.3 summarises the result of each gaze analysis for each experimental condition). While previous studies in the informed forager paradigm indicated gaze as an important cue for both subjects to gauge their opponent's next move and/or to alter one's own next move (Menzel, 1974; Coussi-Korbel, 1994; Hare et al., 2000, 2001; Hirata & Matsuzawa, 2001; Ducoing & Thierry, 2003) they did not specifically examine *how* either subject used gaze (or which type—*static* or *onset*) to inform those decisions.

TABLE 6.3: Overall summary of different gaze following types throughout the experiment, Pair 1 (Results listed in Prediction/Outcome format)

	Overall <i>Competition</i>	<i>No Knowledge</i>	<i>Full Knowledge</i>	<i>No Bait, No Knowledge</i>
Dominant follows Subordinate's <i>static</i> gaze	Yes/Yes	No/Yes	No/No	No/Yes
Subordinate follows Dominant's <i>static</i> gaze	No/No	No/Yes	No/Yes	No/No
Dominant follows Subordinate's gaze <i>onset</i>	Yes/Yes	No/No	No/No	No/Yes
Subordinate follows Dominant's gaze <i>onset</i>	No/Yes	No/Yes	No/Yes	No/Yes

The dominant followed the subordinate's *static* gaze when she had no knowledge of where the bait was located, but when she had seen the bait hidden she did not follow the subordinate's *static* gaze, or *gaze onset*; she ran to retrieve the bait without looking to the subordinate for visual cues. Similarly, the subordinate followed the dominant's *static* gaze except when only she had privileged information regarding its location during the *Competition*. Without information about the bait's location, each subject followed her opponent's gaze; when she did have information, neither subject followed the other's *static* gaze.

The subordinate followed changes in the dominant's gaze, i.e., a *gaze onset*, at all times. This contrasts with the subordinate's behaviour of *static* gaze following: she did not follow the dominant's *static* gaze in the *Competition*, though she did through the three control conditions. Puzzlingly, the dominant did not follow the subordinate's *gaze onset* when neither chimpanzee had knowledge of the bait; yet the dominant followed *gaze onset* during the *Competition* and *No Bait, No Knowledge* trials. However, during the *No Knowledge* trials the dominant may not have followed the subordinate's *gaze onset* because it apparently no longer provided valuable information (the subordinate only found one banana during the four trials). Another possibility is that the subordinate did not behave as if she was actively searching for a hidden food item, and so the dominant was less motivated to follow her *gaze onset*, but this would not explain why the dominant did follow the subordinate's *static* gaze. In the *No Knowledge* trials, the dominant did not follow in the subordinate's *footsteps* (see Chapter 5: Movement Following), and this was found to be the only movement type positively associated with following *gaze onset* in this pair. Therefore it seems that by not using this movement type, the dominant was less likely to follow *gaze onset*.

The *No Bait, No Knowledge* controls were implemented to determine if the dominant would continue using exploitative tactics (movement following and gaze following) in the absence of a hidden banana. After thirty-two trials in which a banana had been hidden in the enclosure, it is possible that the chimpanzees learned that searching for a reward despite not knowing its location was a good tactic, one they did not abandon as expected during this control. Both subjects used both gaze following types; however, a notable difference was that (unlike in the case of the *Competition*) the subordinate followed the dominant's *static* gaze.

When gaze was analysed in conjunction with movement types, the dominant followed the subordinate's *static* gaze when following by any of the three different definitions of

movement following, but only followed the subordinate's gaze *onset* while walking in her *footsteps*. The subordinate followed the dominant's *static* gaze while *approaching*, and followed gaze using both gaze types while walking in the dominant's *footsteps*.

When the dominant *approached* the subordinate as a tactic to exploit the subordinate's foraging success, the subordinate reacted by stopping her walk towards the bait (stopping immediately after the dominant *approached* in Phase 3; see Figure 5.16). When the subordinate stopped walking she also stopped gazing towards the bait for at least five seconds. Thus, the subordinate countered the dominant's exploitation in two ways: the subordinate was not only capable of restraining her desire to continue walking to retrieve the banana, but also capable of withholding her gaze towards the area of the enclosure where it was hidden, so that the dominant could not follow the subordinate's gaze and then move in that direction (see also Goodall, 1971, cited as record #213 in Byrne & Whiten, 1990). This is excellent evidence for first-order tactical deception (Mitchell, 1986; Whiten & Byrne, 1988).

V. Results: Pair 2, Reinette and Georgia

In this section the same analyses are repeated for the second pair of chimpanzees, subordinate Reinette and dominant Georgia, to test the ideas that were developed with the first pair. The comparison of both pairs will illuminate ways in which gaze is used in the informed forager paradigm by each subject, and differences between the two pairs' tactics. I present correlograms of both chimpanzees gazing towards the bait and then towards absolute quadrants. I then present an analysis of each subject's use of the two defined gaze following types, and how they relate to the three movement following types defined in Chapter 5. I asked the same questions as above: Did the dominant gaze towards the bait after the subordinate gazed towards the bait, and does this pattern extend to other areas of the enclosure? Does each subject follow the other's *static* gaze, and her gaze *onset*? How does gaze following relate to movement following?

A. Analysis of Gazing Towards the Bait During *Competition*

The subordinate competitor saw where the bait was hidden on each trial, but the dominant did not. If the dominant followed the subordinate's gaze, one would expect to see in the correlogram a peak after the referent behaviour at time= 0 (see the analysis of Pair 1 described in Chapter 4: Statistical Methods). However, here the peak in the correlogram occurs at time= -1, one second *before* the subordinate starts gazing towards the bait (Figure

6.36; graphs for *No Knowledge* and *Full Knowledge* controls are included in the appendix to Chapter 6). Figure 6.36 shows that the dominant was looking towards the bait significantly more than expected before the subordinate began to look in that direction.

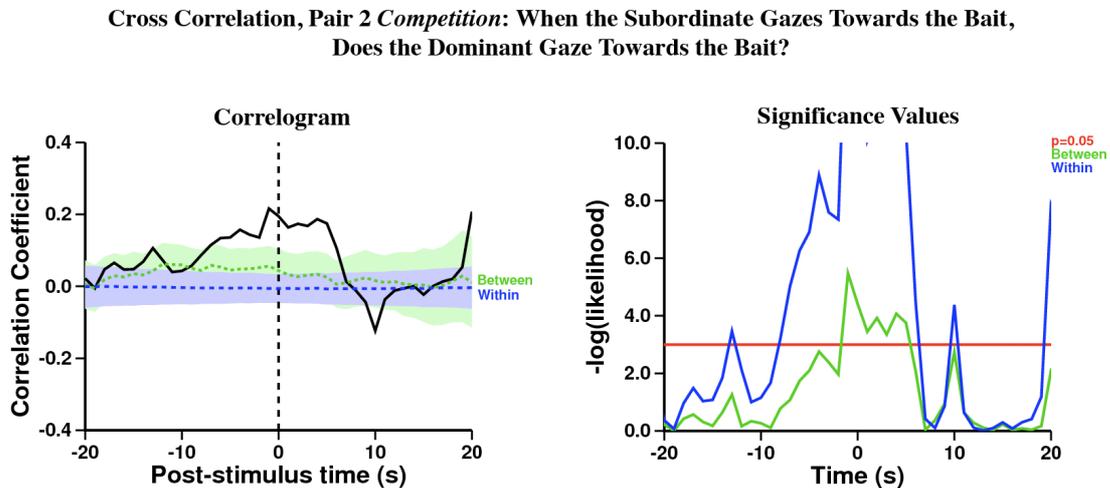


FIGURE 6.36: Referent behaviour: subordinate gazing towards the bait. Target behaviour: dominant gazing towards the bait. When the subordinate gazed towards the bait, the dominant gazed towards the bait significantly more than expected from the within-trial shuffled control (peak at time= -1, $r = 0.2161$, $n = 616$; $-\log\text{-likelihood} = 16.7621$, $p < 0.05$).

When the reverse situation is analysed (i.e., whether the subordinate looked towards the bait after the dominant started looking towards it), it appears that the subordinate had already been gazing towards the bait by the time the dominant started to gaze. The data in Figure 6.37 below are the same as in Figure 6.34 above: the cross correlation with the referent and target swapped results in a graph that is reversed in time along the x-axis. The correlograms portray the duration of an action, and it appears in this case that both chimpanzees begin to gaze towards the bait at around the same time, for a similar duration (compare Figures 6.36 and 6.37).

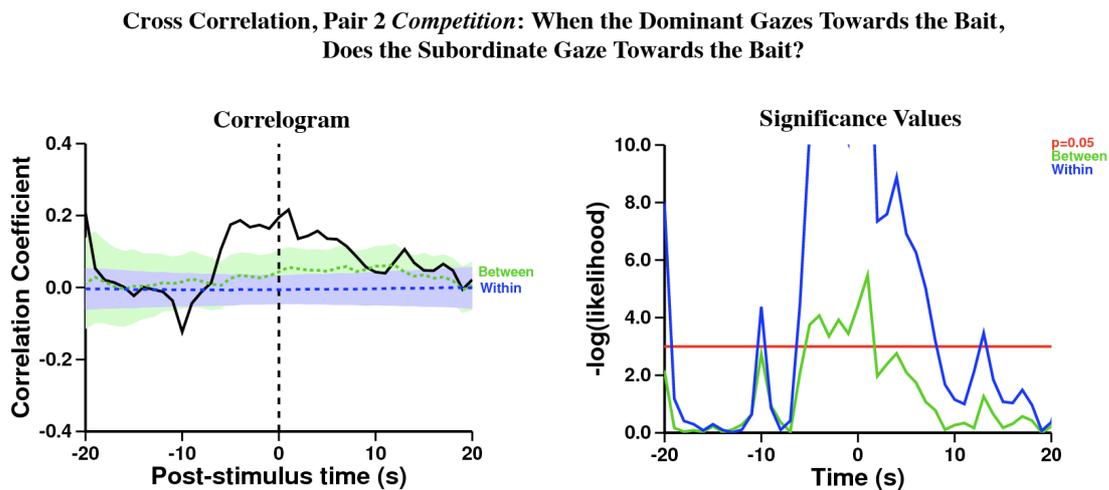


FIGURE 6.37: Referent behaviour: dominant gazing towards the bait. Target behaviour: subordinate gazing towards the bait. After the dominant started gazing towards the bait at time= 0, the subordinate had already been gazing towards it significantly more than expected from the within-trial shuffled control.

Since both chimpanzees gazed towards the bait (together) significantly more than expected it will be worthwhile to investigate if this pattern is the same for absolute directions in their enclosure. This may allow us to determine whether their gaze was due to some cue provided by the bait (e.g., an olfactory cue) or whether both chimpanzees gazed at the same time in other directions regardless of the location of the bait.

B. Analysis of Gazing Towards Absolute Directions During *Competition*

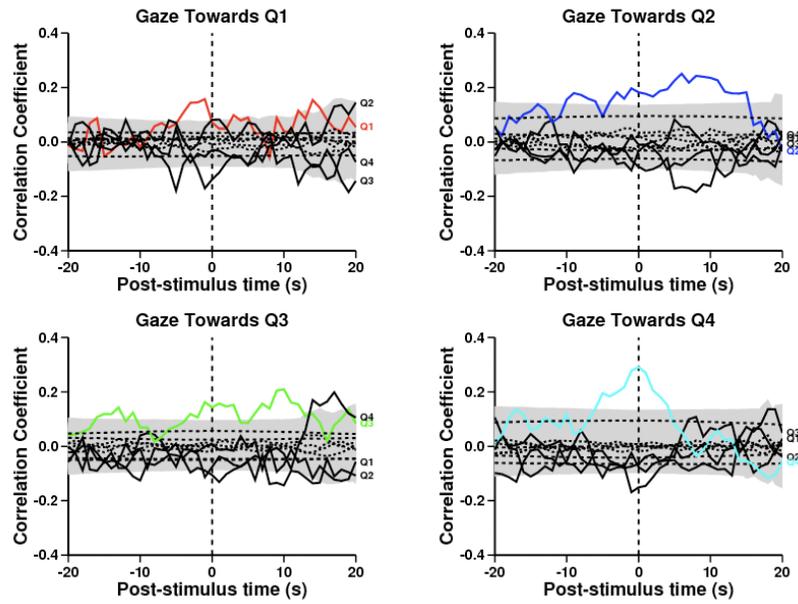
I analysed whether the dominant and subordinate gazed to absolute locations in the enclosure at the same time, regardless of the location of the bait, by asking, “When the subordinate gazes towards a quadrant, towards which quadrant does the dominant gaze?” I compared the subordinate’s gaze towards one quadrant with the dominant’s likelihood of gazing towards any of the four quadrants (Figure 6.38). When the subordinate gazed towards a certain quadrant the dominant gazed towards the *same* quadrant as the subordinate, rather than any other quadrant, significantly more than expected from the between-trial shuffled control. It appears that the dominant gazed towards Quadrant 1 significantly more than expected *before* the subordinate gazed towards Q1, which may be an artefact of the experimental setup in which the dominant entered the enclosure before the subordinate. After the subordinate gazed towards Q2, the dominant gazed towards Q2 more than towards any other quadrant, while for Q3 and Q4, the dominant gazed towards the same quadrant at the same time. Thus for three quadrants, after the subordinate gazed towards an absolute

direction the dominant gazed towards the same absolute direction, when the location of the bait was not taken into account. It is, however, clear that there is a very strong influence of gazing towards Q4 as the correlation coefficients for both chimpanzees gazing in that direction are much higher than for other quadrants. This may again be a result of the layout of the enclosure and the chimpanzees' pattern of movement towards it as discussed in Chapter 5: Movement Following.

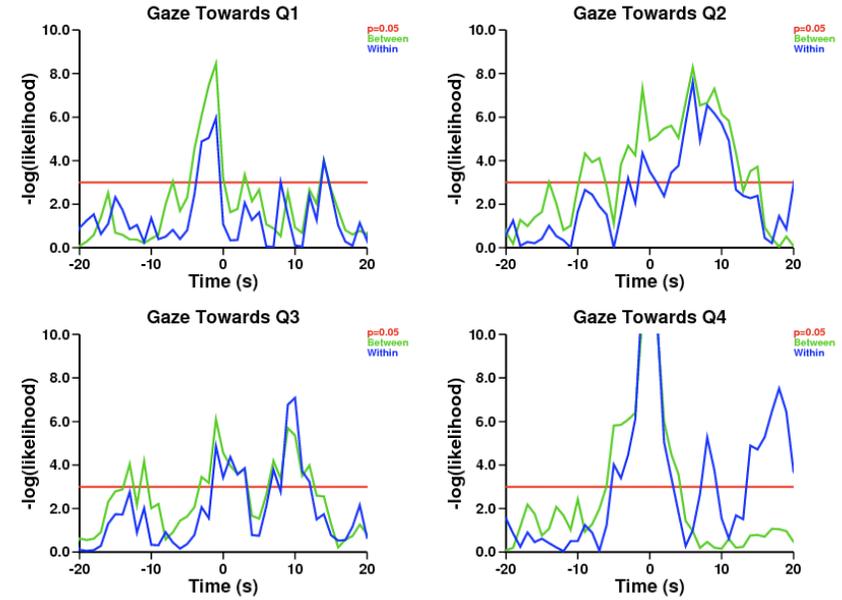
FIGURE 6.38 (next page): In each panel, the referent behaviour at time= 0 is the subordinate gazing towards the quadrant of that panel. The coloured line in each panel represents the cross correlation of the dominant gazing towards the same quadrant as the subordinate. The three solid black lines represent the cross correlation of the dominant gazing towards each of the other three quadrants. The dotted lines with the gray spread represent the within- and between-trial shuffled controls and their standard errors of the mean. For example, in the top left panel, the referent behaviour at time= 0 is the subordinate gazing towards Q1 and it is correlated with the target behaviour of the dominant gazing towards Q1, and this relationship is plotted with a red line. The black lines show the cross correlations of the subordinate gazing towards Q1 with the dominant gazing towards Q2, Q3, and Q4. Before the subordinate started gazing towards Q1 (time= -1, $r = 0.1574$, $n = 619$; $-\log$ -likelihood= 8.4606, $p < 0.05$), after the subordinate started gazing towards Q2 (time= +6, $r = 0.2510$, $n = 482$; $-\log$ -likelihood= 8.2801, $p < 0.05$), before and after the subordinate gazed towards Q3 (time= -1, $r = 0.1629$, $n = 619$; $-\log$ -likelihood= 6.0955, $p < 0.05$. time= +7, $r = 0.1568$, $n = 460$; $-\log$ -likelihood= 4.1895, $p < 0.05$), and at the moment that the subordinate gazed to Q4 (time= 0, $r = 0.2912$, $n = 615$; $-\log$ -likelihood= 12.1821, $p < 0.05$), the dominant gazed towards the same quadrant as the subordinate significantly more than expected from the between-trial shuffled control.

Cross Correlations, Pair 2 *Competition*: When the Subordinate Gazes Towards a Quadrant, Towards Which Quadrant Does the Dominant Gaze?

Correlograms



Significance Values



C. Time Spent Gazing Towards Each Quadrant During *Competition*

I calculated the percent of time that each chimpanzee spent gazing at each of the four quadrants of their enclosure to determine if their gaze patterns were equally distributed or influenced by their asymmetrical movement patterns (see Chapter 5: Movement Following). Dominant Georgia gazed less frequently towards Q2 than towards the other quadrants, and subordinate Reinette gazed least towards Q4 (Table 6.4).

TABLE 6.4: Percent of time each subject gazed towards each quadrant, Pair 2

Quadrant	Reinette Gaze	Georgia Gaze
Q1	30.98%	24.28%
Q2	24.64%	13.12%
Q3	23.63%	34.91%
Q4	20.03%	26.77%
0 (Unknown)	0.72%	0.92%

Overall, when the subjects' gaze was recorded at the same time (67.43% of all trials), both gazed together towards the same quadrant 36.91% of the time. Of this total time gazing towards the same quadrant, they spent approximately equal amounts of time gazing towards every quadrant except Q2, to which they gazed less overall (Table 6.5).

TABLE 6.5: Percent of time that both chimpanzees gaze towards each quadrant, of the overall time spent gazing together towards the same quadrant, Pair 2

Quadrant	Time
Q1	28.19%
Q2	15.86%
Q3	28.19%
Q4	27.75%
0 (Unknown)	0%

The dominant spent the majority of her time on the left side of the compound (Quadrants 1 and 3), and the subordinate spent the majority of her time in the areas closest to the 'Cognition Room' (Quadrants 3 and 4) (see Chapter 5: Movement following). The chimpanzees did not, however, spend a proportionate amount of time gazing at those quadrants. One may expect subjects to gaze towards their current location or towards the same direction that they are moving; the subordinate gazed to the quadrant she was currently in 37.67% of the time and towards the quadrant to which she was headed 40.62% of the time,

and the dominant gazed to the quadrant she was currently in 50.00% of the time and towards the quadrant to which she was headed 37.25% of the time. Each subject's gaze was often incongruent with her direction of movement, approximately 50% of total recorded gazes.

Since this chapter covers gaze interactions between the two chimpanzees, it is important to note that each subject spent differing amounts of time looking at her opponent: the subordinate looked at the dominant for 43.92% of the time that her gaze direction was recorded, and the dominant looked at the subordinate for 23.33% of the time that her gaze was recorded, consistent with Chance's (1967) predictions.

Whether the chimpanzees' gazing behaviour is analysed in terms of relative position in the enclosure (e.g., towards the bait) or in terms of absolute direction (e.g., towards Q2), both chimpanzees gazed towards the same location at approximately the same time: it was unclear upon whose gaze cue the other subject gazed in a certain direction. The exception was when they gazed towards Q1: the dominant was more likely to gaze towards Q1 before the subordinate, perhaps an artefact of the experimental setup as the dominant entered the enclosure before the subordinate, and may have been looking ahead of herself towards Q1. Overall, the general pattern of gazing towards the same quadrant at the same time may indicate that the chimpanzees followed each other's gaze, so I investigated two types of gaze following, *static* and *onset*.

D. *Static* Gaze Following

Here I describe whether each subject followed her opponent's *static* gaze, using cross correlation analysis. Recall that *static* gaze following is defined as "one individual looks at the other and then both chimpanzees gaze towards the same quadrant." I first address whether the dominant followed the subordinate's *static* gaze, and then whether the subordinate followed the dominant's, for the entire *Competition* dataset (graphs showed consistent patterns across each of the three phases, so individual Phase graphs are included in the appendix to Chapter 6), then the *No Knowledge*, *Full Knowledge*, and *No Bait, No Knowledge* controls.

1. Entire *Competition* dataset

Both before and after the dominant looked at the subordinate, both chimpanzees were gazing towards the same quadrant (Figure 6.39).

Cross Correlation, Pair 2 *Competition*: When the Dominant Looks at the Subordinate, Do They Both Gaze Towards the Same Quadrant?

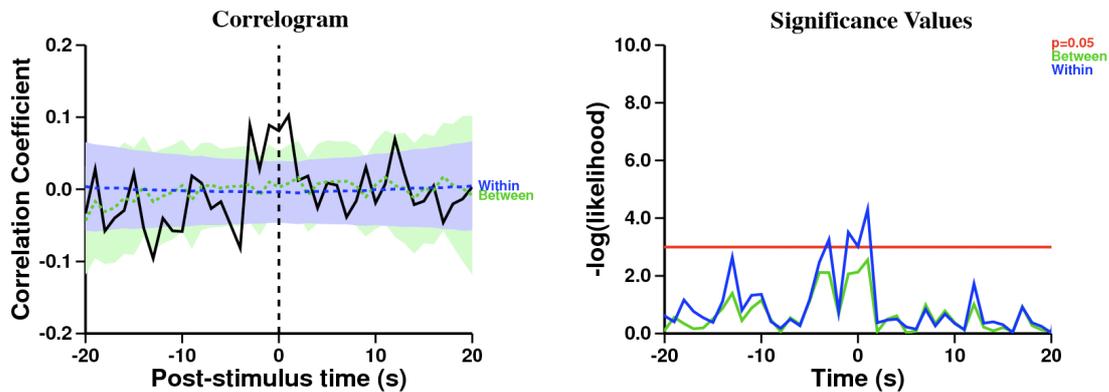


FIGURE 6.39: Referent behaviour: dominant looking at subordinate. Target behaviour: both chimpanzees gazing towards the same quadrant. Before and after the dominant looked at the subordinate, both chimpanzees gazed towards the same quadrant significantly more than expected from the within-trial shuffled control (peak at time= +1, $r = 0.1023$, $n = 613$; $-\log\text{-likelihood} = 4.3030$, $p < 0.05$).

On the other hand, when the subordinate looked at the dominant, it was not until thirteen seconds later, on average, that both chimpanzees gazed towards the same quadrant (Figure 6.40). This large time scale indicates that the relationship is more of a coincidence than a functional following relationship, since most glances were no more than a few seconds.

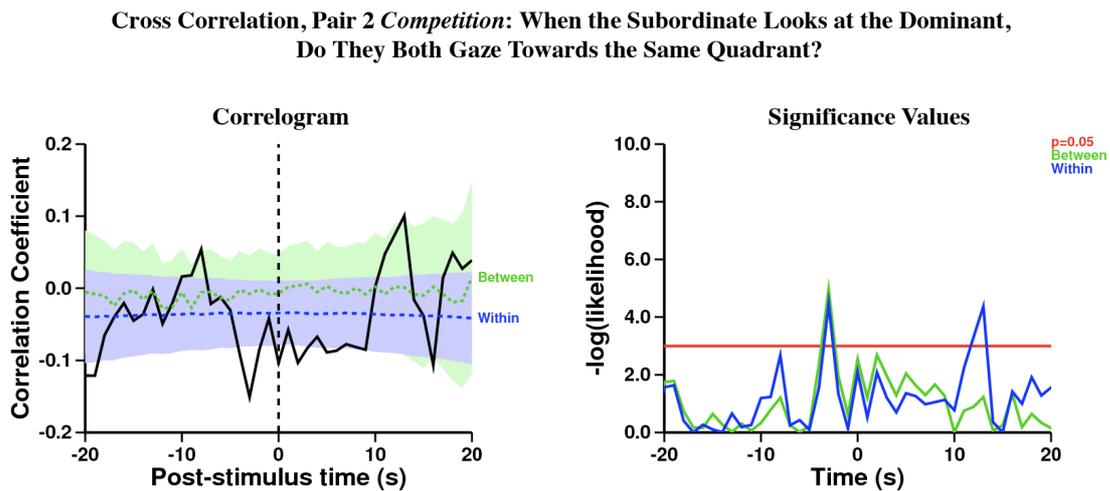


FIGURE 6.40: Referent behaviour: subordinate looking at dominant. Target behaviour: both chimpanzees gazing towards the same quadrant. Before the subordinate looked at the dominant, the chimpanzees were significantly unlikely to look towards the same quadrant (peak at time= -3, $r = -0.1510$, $n = 542$; $-\log\text{-likelihood} = 4.4601$, $p < 0.05$). Many seconds after the subordinate looked at the dominant, both chimpanzees gazed towards the same quadrant significantly more than expected from the within-trial shuffled control (peak at time= +13; $r = 0.1004$, $n = 291$; $-\log\text{-likelihood} = 4.3676$, $p < 0.05$).

Though the subordinate spent a considerable amount of time looking directly at the dominant—nearly 44% of her total recorded gazes—she did not seem to follow the dominant’s direction of *static* gaze with any urgency. This pattern remained consistent through all three phases (see appendix to Chapter 6).

2. *No Knowledge* controls

Since neither chimpanzee had seen where the bait was hidden in the *No Knowledge* controls, I did not expect there to be a difference between their *static* gaze following patterns. Both chimpanzees were significantly likely to be gazing towards the same quadrant both before and after the dominant looked at the subordinate (Figure 6.41).

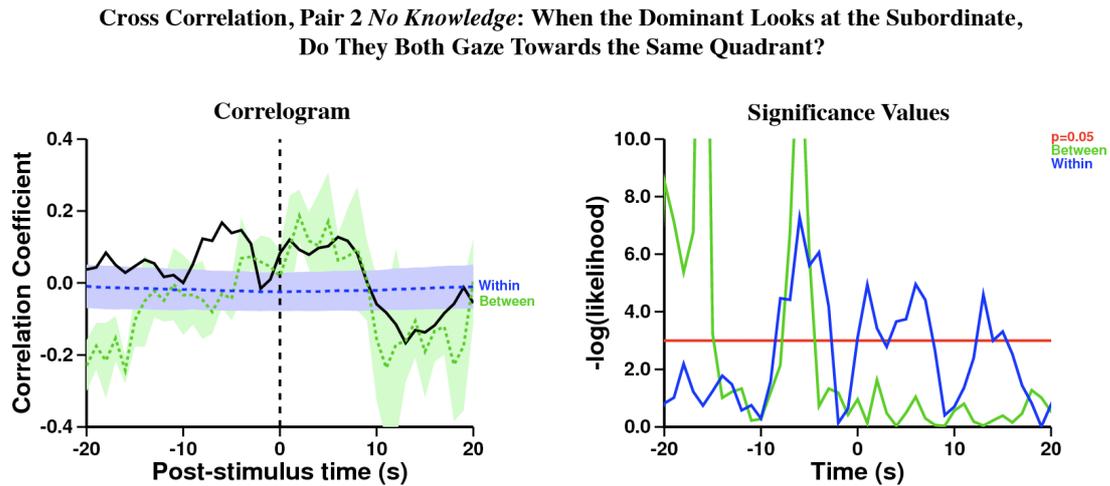


FIGURE 6.41: Referent behaviour: dominant looking at subordinate. Target behaviour: both chimpanzees gazing towards the same quadrant. Before and after the dominant looked at the subordinate, both chimpanzees were gazing towards the same quadrant (peak at time= -6, $r=0.1676$, $n=316$; $-\log\text{-likelihood}=7.2812$, $p<0.05$). Peak at time= +6, $r=0.1276$, $n=319$; $-\log\text{-likelihood}=4.9549$, $p<0.05$). Many seconds later, the chimpanzees were significantly unlikely to be gazing in the same direction (peak at time= +13, $r=-0.1669$, $n=291$; $-\log\text{-likelihood}=4.5938$, $p<0.05$).

The subordinate also followed the dominant's *static* gaze, though it is notable that after the subordinate looked at the dominant, they both gazed towards the same quadrant significantly more than expected within six seconds (Figure 6.42); this is faster than during *Competition* trials, and in the same range as the dominant following the subordinate's gaze in this same *No Knowledge* condition (Figure 6.41).

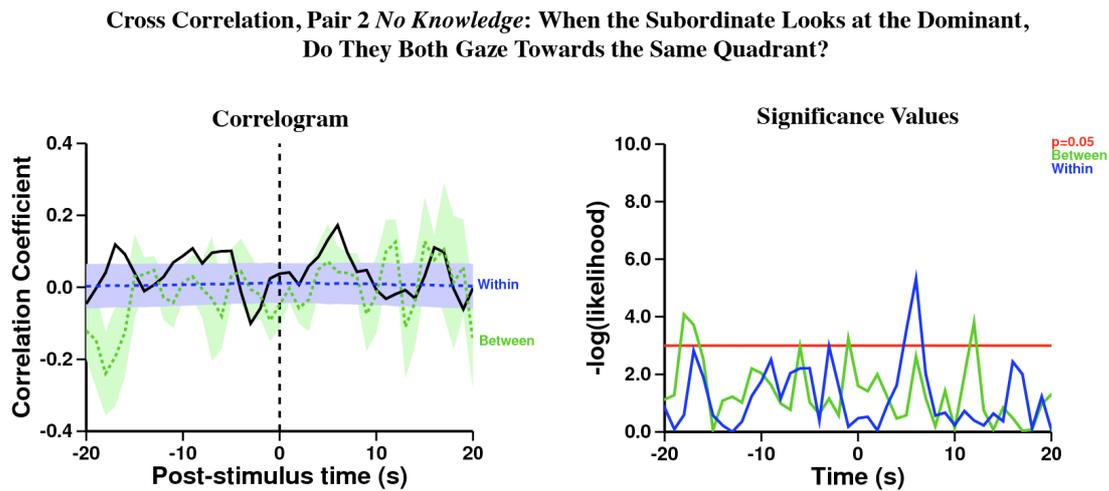


FIGURE 6.42: Referent behaviour: subordinate looking at the dominant. Target behaviour: both chimpanzees gazing towards the same quadrant. After the subordinate looked at the dominant, both chimpanzees gazed towards the same quadrant significantly more than expected from the within-trial shuffled control (peak at time= +6, $r = 0.1723$, $n = 318$; $-\log\text{-likelihood} = 5.3233$, $p < 0.05$).

Though there was no possible information to be gained from the opponent regarding the location of the hidden food, both subjects followed each other's *static* gaze.

3. Full Knowledge controls

The dominant ran directly to retrieve the bait on every trial in the *Full Knowledge* condition, and there is no evidence that she followed the subordinate's *static* gaze (Figure 6.43).

Cross Correlation, Pair 2 *Full Knowledge*: When the Dominant Looks at the Subordinate, Do They Both Gaze Towards the Same Quadrant?

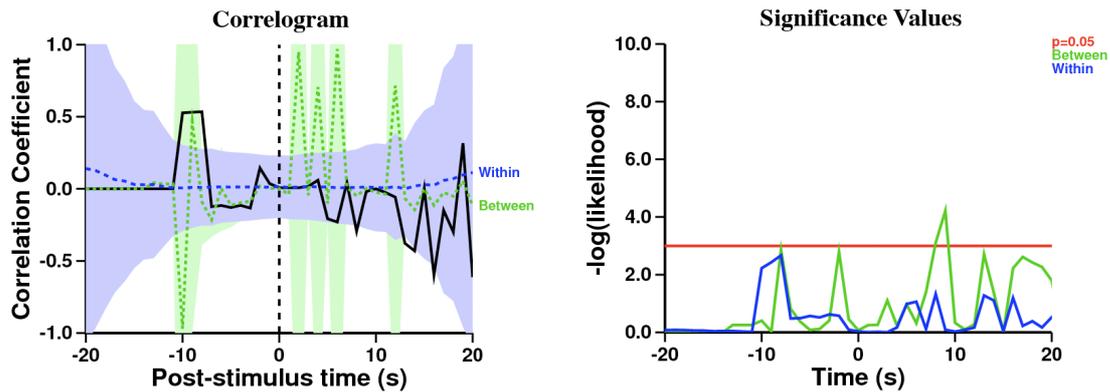


FIGURE 6.43: Referent behaviour: dominant looking at subordinate. Target behaviour: both chimpanzees gazing towards the same quadrant. Before the dominant looked at the subordinate, both chimpanzees gazed towards the same quadrant, but afterward there was no relationship (peak at time= -8, $r = 0.5345$, $n = 15$; $-\log(\text{likelihood}) = 2.6683$, *ns*).

The pattern in the correlogram shows that the subordinate gazed towards the same quadrant as the dominant both before and after looking at the dominant, though the relationship was not significant (Figure 6.44).

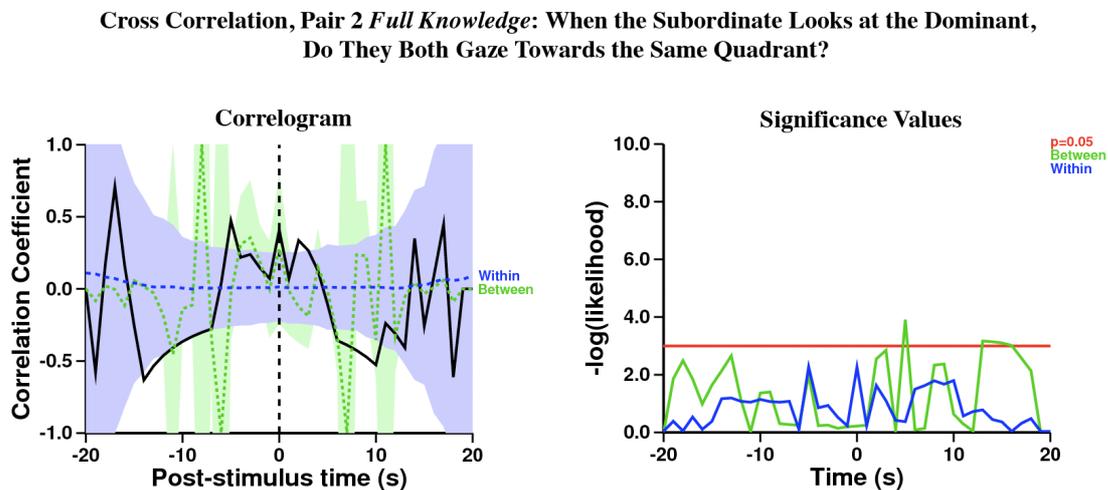


FIGURE 6.44: Referent behaviour: subordinate looks at dominant. Target behaviour: both chimpanzees gazing towards the same quadrant. Before and at the moment that the subordinate looked at the dominant, both chimpanzees gazed in the same direction (peak at time= -5, $r = 0.4725$, $n = 18$; $-\log\text{-likelihood} = 2.2754$, *ns*. Peak at time= 0, $r = 0.4095$, $n = 31$; $-\log\text{-likelihood} = 2.2667$, *ns*). After the subordinate looked at the dominant, the chimpanzees were less likely to gaze towards the same quadrant (peak at time= +10, $r = -0.5270$, $n = 13$; $-\log\text{-likelihood} = 1.7976$, *ns*).

4. *No Bait, No Knowledge* controls

During the *No Bait, No Knowledge* controls, both chimpanzees were likely to be gazing towards the same quadrant before the dominant looked towards the subordinate, though this relationship was only significant for a brief period and may not reflect an ecologically meaningful relationship (Figure 6.45).

Cross Correlation, Pair 2 *No Bait, No Knowledge*: When the Dominant Looks at the Subordinate, Do They Both Gaze Towards the Same Quadrant?

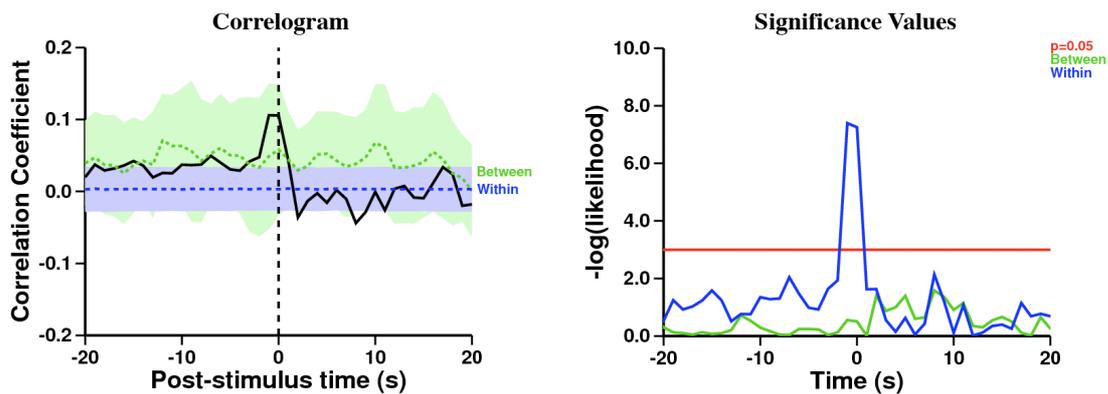


FIGURE 6.45: Referent behaviour: dominant looking at subordinate. Target behaviour: both chimpanzees gazing towards the same quadrant. Before the dominant looked at the subordinate, the chimpanzees gazed towards the same quadrant significantly more than expected from the within-trial shuffled control (peak at time= -1, $r = 0.1059$, $n = 986$; $-\log\text{-likelihood} = 7.3943$, $p < 0.05$).

At the moment that the subordinate looked at the dominant, both were gazing towards the same quadrant, but a few seconds later the chimpanzees gazed towards the same quadrant significantly less than expected from the within-trial shuffled control (Figure 6.46).

**Cross Correlation, Pair 2 No Bait, No Knowledge: When the Subordinate Looks at the Dominant,
Do They Both Gaze Towards the Same Quadrant?**

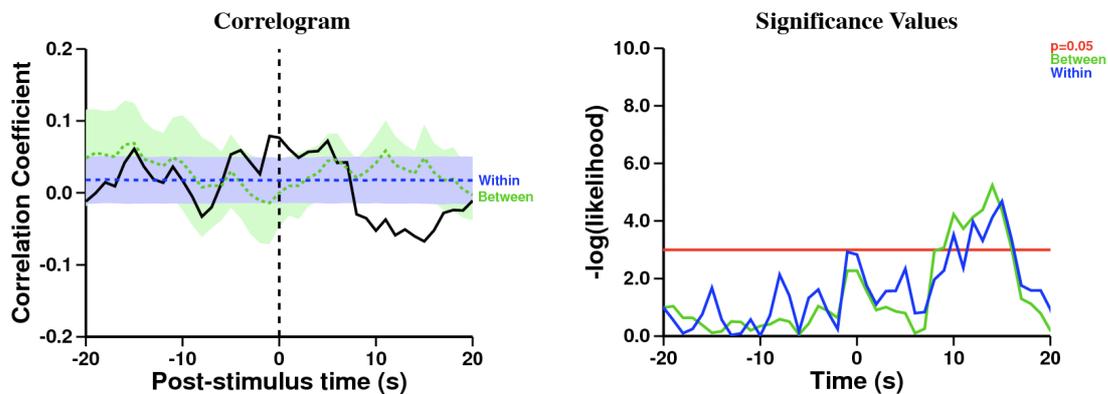


FIGURE 6.46: Referent behaviour: subordinate looking at dominant. Target behaviour: both chimpanzees gazing towards the same quadrant. Before the subordinate looked at the dominant, both chimpanzees gazed towards the same quadrant (peak at time= -1, $r = 0.0790$, $n = 903$; $-\log\text{-likelihood} = 2.9216$, *ns*). After the subordinate looked at the dominant, the chimpanzees did not gaze towards the same quadrant (peak at time= +15, $r = -0.0674$, $n = 866$; $-\log\text{-likelihood} = 4.6851$, $p < 0.05$).

5. Summary of *Static* Gaze Following behaviour

During the *Competition*, both chimpanzees gazed towards the same quadrant both before and after the dominant looked at the subordinate. In contrast, after the subordinate looked at the dominant, both chimpanzees gazed towards the same quadrant thirteen seconds later, which is likely to be more of a coincidence than a functional *gaze following* relationship. This pattern was consistent throughout the *Competition*, so it cannot be explained by the dominant's movement following behaviour: one might expect that if the dominant were walking directly behind the subordinate she would be faster to follow the subordinate's gaze than the opposite scenario, but the dominant's movement following tactics changed over the course of the competition, such that by Phase 3 she was neither *approaching* nor following in the subordinate's *footsteps* (See Chapter 5: Movement Following). Additionally, the subordinate did appear to follow the dominant on many trials, so if the speed of her gaze were related to movement following I would expect a shorter delay between looking at the dominant and then gazing towards the same quadrant.

When the dominant had seen where the bait was hidden on the *Full Knowledge* trials, she did not follow the subordinate's gaze, suggesting that her gaze following on *Competition*

trials was a tactic to gain information from the subordinate about her direction of gaze and movement.

In the *No Knowledge* condition, the dominant's gaze following behaviour was essentially the same as in the *Competition* trials. The subordinate followed the dominant's gaze in this condition. In the *No Bait, No Knowledge* trials, however, neither chimpanzee followed *static* gaze.

E. Following Gaze Onset

Here I present results of each subject following her opponent's gaze *onset*, which was defined as "one individual changes her gaze direction in view of the other, and then both chimpanzees gaze towards the same quadrant." I first address whether the dominant followed the subordinate's gaze *onset*, and then whether the subordinate followed the dominant's, for the entire *Competition* dataset, then the *No Knowledge*, *Full Knowledge*, and *No Bait, No Knowledge* controls. Graphs showed consistent patterns across each of the three phases of the *Competition*, and so individual Phase graphs are included in the appendix to Chapter 6.

1. Entire *Competition* dataset

After the subordinate changed her gaze direction while in view of the dominant, the chimpanzees did not both gaze towards the same quadrant; the dominant did not follow the subordinate's gaze change to a new direction (Figure 6.47).

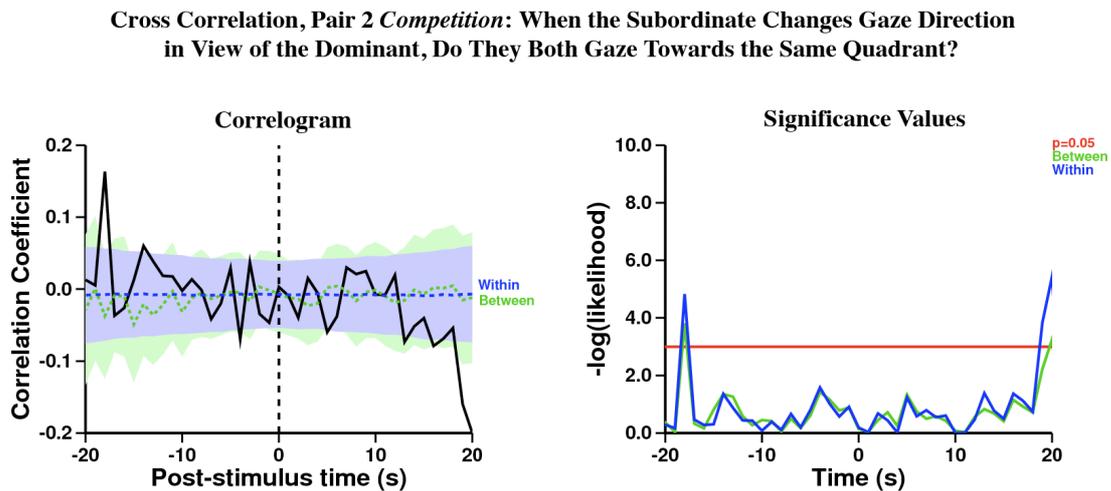


FIGURE 6.47: Referent behaviour: subordinate changes gaze direction in view of the dominant. Target behaviour: both chimpanzees gazing towards the same quadrant. There is no relationship between the two variables. At either end of the correlogram, the relationship becomes significant: before the subordinate changed her gaze the chimpanzees gazed towards the same quadrant (peak at time= -18, $r = 0.1633$, $n = 223$; $-\log\text{-likelihood} = 4.8274$, $p < 0.05$), and long after the subordinate changed her gaze direction the chimpanzees did not gaze towards the same quadrant (peak at time= +20, $r = -0.2006$, $n = 168$; $-\log\text{-likelihood} = 5.4322$, $p < 0.05$).

When the dominant changed her gaze direction while in view of the subordinate, the chimpanzees gazed towards the same quadrant significantly less than expected from the within-trial shuffled control; the subordinate did not follow the dominant's change in gaze direction (Figure 6.48). Several seconds later, the likelihood that they both gazed towards the same quadrant increased, but this relationship remained non-significant.

Cross Correlation, Pair 2 *Competition*: When the Dominant Changes Gaze Direction in View of the Subordinate, Do They Both Gaze Towards the Same Quadrant?

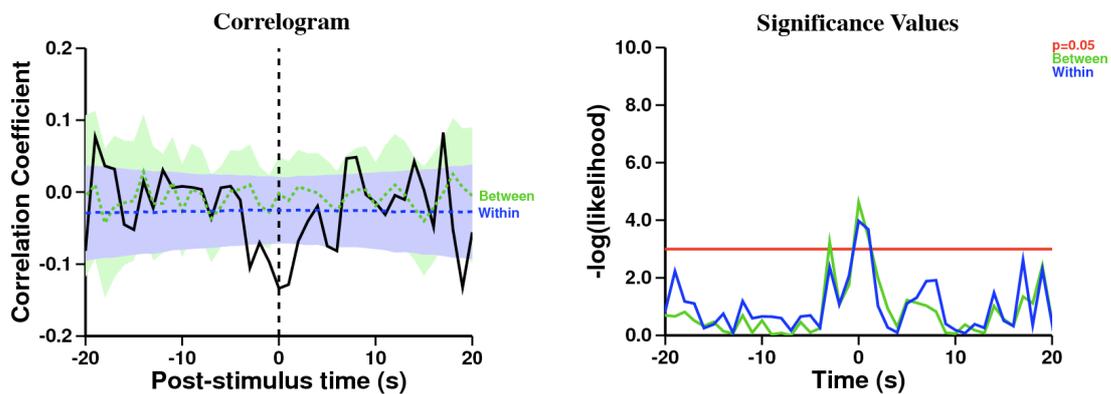


FIGURE 6.48: Referent behaviour: dominant changes her gaze direction in view of the subordinate. Target behaviour: both chimpanzees gazing towards the same quadrant. At the moment that the dominant changed her gaze, the chimpanzees gazed towards the same quadrant significantly less than expected from the within-trial shuffled control (peak at time= 0, $r = -0.1338$, $n = 597$; $-\log\text{-likelihood} = 3.9734$, $p < 0.05$). Several seconds later, the relationship trends towards being more than expected from the within-trial shuffled control (peak at time= +8, $r = 0.0485$, $n = 421$; $-\log\text{-likelihood} = 1.9137$, ns).

2. *No Knowledge* controls

The results of following gaze *onset* for both subjects in the *No Knowledge* controls are similar to each other: both chimpanzees were likely to be gazing towards the same quadrant before the either the dominant or the subordinate changed her gaze direction, but after a gaze change, neither subject followed her opponent's gaze *onset* (Figures 6.49 and 6.50).

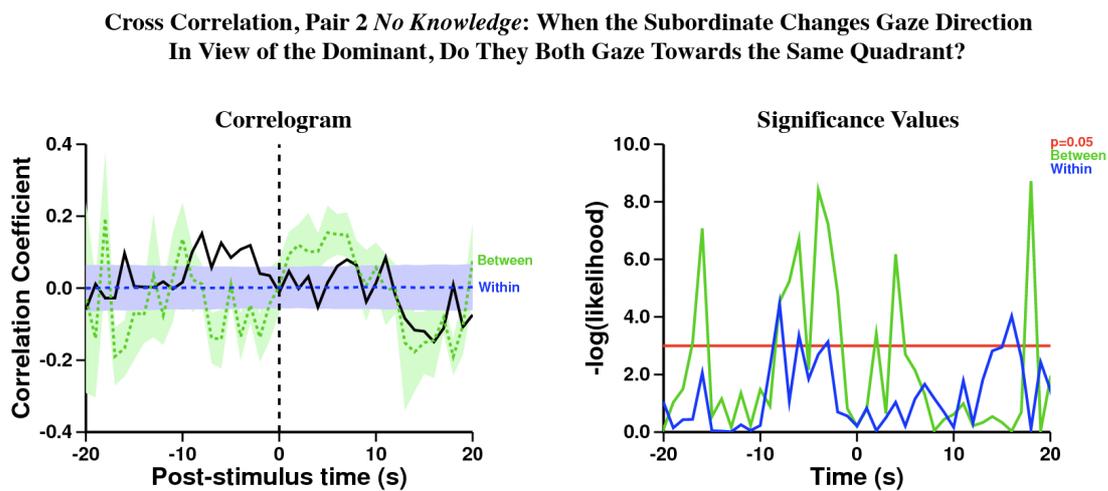


FIGURE 6.49: Referent behaviour: subordinate changes gaze direction in view of the dominant. Target behaviour: both chimpanzees gazing towards the same quadrant. Before the subordinate changed her gaze, both chimpanzees gazed towards the same quadrant significantly more than expected from the within-trial shuffled control (peak at time= -8, $r=0.1518$, $n=293$; $-\log\text{-likelihood}=4.4549$, $p<0.05$). There is no relationship after the subordinate's gaze change until 16 seconds later, when the chimpanzees did not gaze towards the same quadrant (peak at time= +16, $r=-0.1493$, $n=248$; $-\log\text{-likelihood}=4.0287$, $p<0.05$).

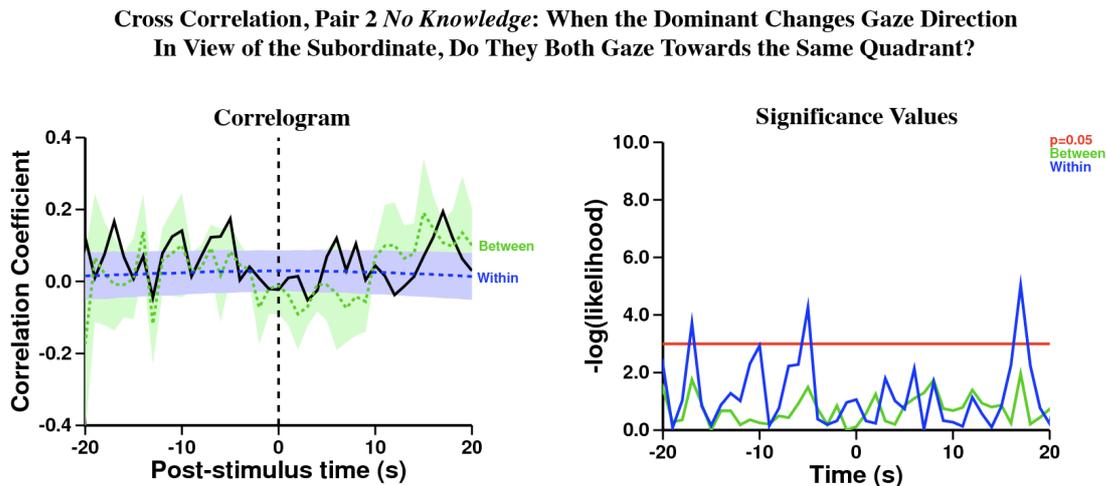


FIGURE 6.50: Referent behaviour: dominant changes gaze direction in view of the subordinate. Target behaviour: both chimpanzees gazing towards the same quadrant. Before and after the dominant changed her gaze, both chimpanzees gazed towards the same quadrant (peak at time= -5, $r= 0.1744$, $n= 301$; $-\log\text{-likelihood}= 4.2629$, $p<0.05$. Peak at time= +17, $r= 0.1939$, $n= 242$; $-\log\text{-likelihood}= 5.0287$, $p<0.05$).

3. Full Knowledge controls

When the subordinate changed her gaze direction in view of the dominant during the *Full Knowledge* trials, both chimpanzees were significantly likely to gaze towards the same quadrant for a very brief moment (Figure 6.51).

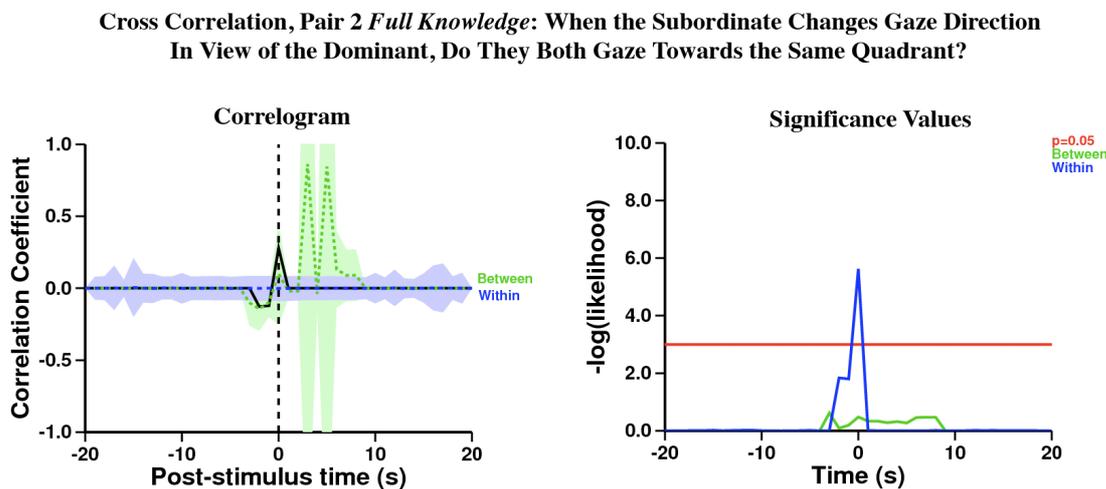


FIGURE 6.51: Referent behaviour: subordinate changes gaze direction in view of the dominant. Target behaviour: both chimpanzees gazing towards the same quadrant. After the subordinate changed her gaze, both chimpanzees gazed towards the same quadrant significantly more than expected from the within-trial shuffled control (peak at time= 0, $r= 0.2796$, $n= 28$; $-\log\text{-likelihood}= 5.6238$, $p<0.05$).

Both chimpanzees gazed towards the same quadrant before the dominant changed her gaze direction in view of the subordinate, after which both subjects did not gaze in the same direction (Figure 6.52).

**Correlation Coefficient, Pair 2 Full Knowledge: When the Dominant Changes Gaze Direction
In View of the Subordinate, Do They Both Gaze Towards the Same Quadrant?**

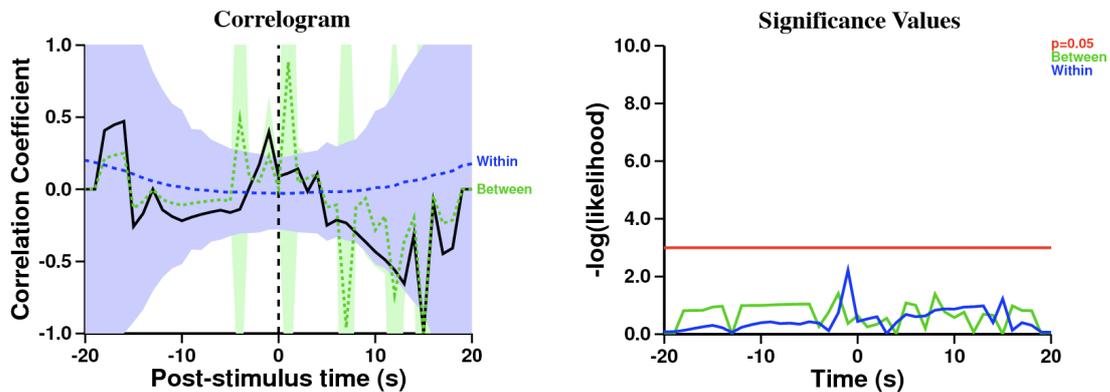


FIGURE 6.52: Referent behaviour: dominant changes gaze direction in view of the subordinate. Target behaviour: both chimpanzees gazing towards the same quadrant. Before the dominant changed her gaze, both chimpanzees gazed towards the same quadrant; this relationship trends towards being more than expected from the within-trial shuffled control (peak at time= -1, $r = 0.3977$, $n = 23$; $-\log\text{-likelihood} = 2.2190$, *ns*).

4. *No Bait, No Knowledge* controls

During the *No Bait, No Knowledge* trials, both chimpanzees were significantly likely to be gazing towards the same quadrant before the subordinate changed her gaze direction, after which both were significantly unlikely to gaze towards the same quadrant (Figure 6.53). The dominant did not follow the subordinate's gaze *onset*.

Cross Correlation, Pair 2 *No Bait, No Knowledge*: When the Subordinate Changes Gaze Direction In View of the Dominant, Do They Both Gaze Towards the Same Quadrant?

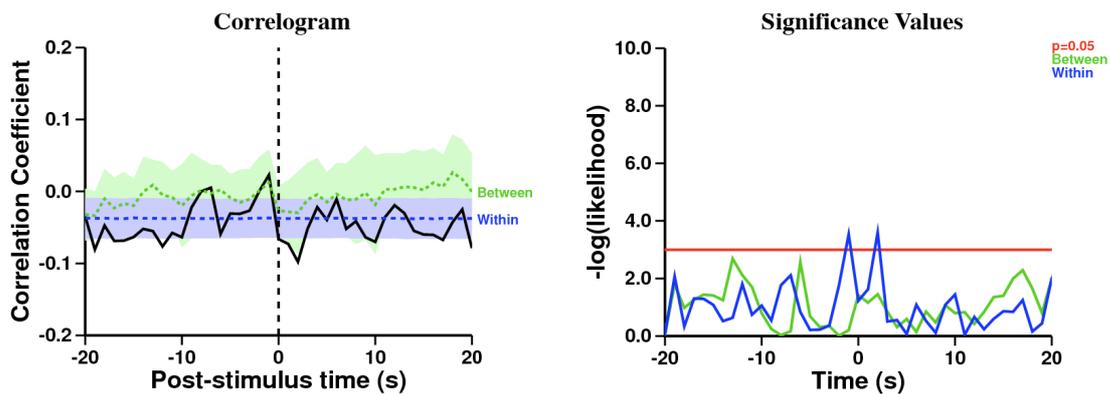


FIGURE 6.53: Referent behaviour: subordinate changes gaze direction in view of the dominant. Target behaviour: both chimpanzees gazing towards the same quadrant. Before the subordinate changed her gaze, both chimpanzees gazed towards the same quadrant (peak at time= -1, $r = 0.0229$, $n = 1140$; $-\log\text{-likelihood} = 3.5309$, $p < 0.05$), but just after the subordinate changed her gaze, they did not gaze towards the same quadrant (peak at time= +2, $r = -0.0978$, $n = 1133$; $-\log\text{-likelihood} = 3.5957$, $p < 0.05$).

Nor did the subordinate follow the dominant's gaze *onset*: after the dominant changed her gaze direction, the chimpanzees were significantly unlikely to gaze towards the same quadrant (Figure 6.54).

Cross Correlation, Pair 2 *No Bait, No Knowledge*: When the Dominant Changes Gaze Direction In View of the Subordinate, Do They Both Gaze Towards the Same Quadrant?

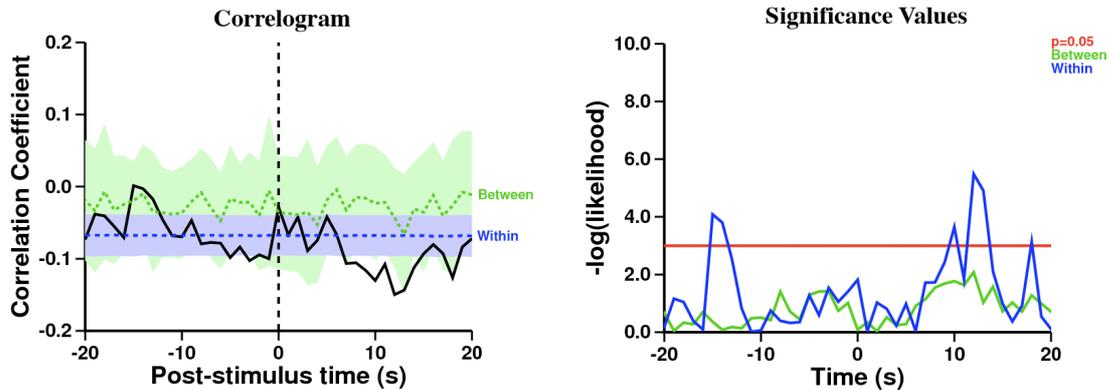


FIGURE 6.54: Referent behaviour: dominant changes gaze direction in view of the subordinate. Target behaviour: both chimpanzees gazing towards the same quadrant. Before the dominant changed her gaze, the chimpanzees gazed towards the same quadrant (peak at time= -15, $r=0.0014$, $n=995$; $-\log\text{-likelihood}=4.0846$, $p<0.05$). Many seconds after the dominant changed her gaze, the chimpanzees did not gaze towards the same quadrant (peak at time= +12, $r=-0.1498$, $n=1007$; $-\log\text{-likelihood}=5.4850$, $p<0.05$).

5. Summary of Following Gaze *Onset* behaviour

Throughout the *Competition*, *No Knowledge*, and *No Bait, No Knowledge* conditions, neither chimpanzee followed the gaze *onset* of their competitor. This is in direct contrast with their *static* gaze following behaviour. In the *Full Knowledge* controls, the dominant very briefly followed the subordinate's gaze *onset*. While monitoring the opponent's gaze *onset* may not have been a common tactic overall, it may have occurred under certain circumstances, so I analysed the relationship between the different types of gaze and the three types of movement following.

F. How Gaze Following Relates to Movement Following

This section will address how gaze relates to the different movement following patterns of each subject: *approach*, *footsteps*, and *converge*. I will address questions such as, does gaze following lead to movement following, or does movement following influence gaze following? Does incongruent gaze precede a change of movement direction? And can gaze cues be withheld?

1. Approach

Following by *approaching*, or walking towards the opponent from a different quadrant, required the dominant to constantly re-adjust her movement in response to the subordinate's current location. To determine the relationship between this type of movement following and gaze following, I asked, "When the dominant *approaches* the subordinate, does the dominant follow the subordinate's *static* gaze?" Though the dominant was unlikely to follow the subordinate's *static* gaze before approaching, after the dominant was in a different quadrant and walking towards the subordinate, she looked at the subordinate and then both chimpanzees gazed towards the same quadrant significantly more than expected (Figure 6.55).

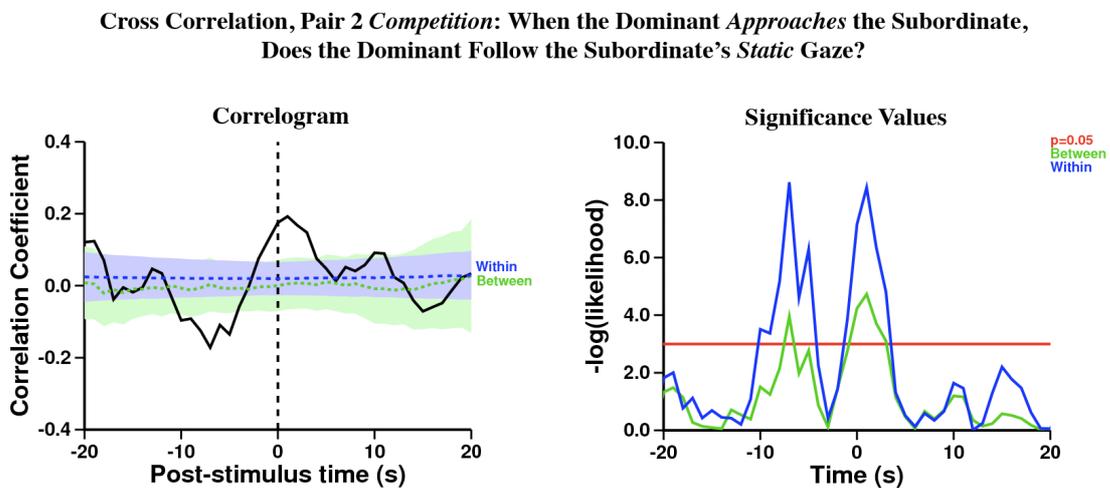


FIGURE 6.55: Referent behaviour: dominant *approaching* the subordinate. Target behaviour: dominant following the subordinate's *static* gaze. After the dominant walked towards the subordinate from a different quadrant, she looked at the subordinate and then both chimpanzees gazed towards the same quadrant significantly more than expected from the within-trial shuffled control (peak at time= +1, $r = 0.1926$, $n = 603$; $-\log\text{-likelihood} = 8.4369$, $p < 0.05$). Before the dominant *approached* the subordinate, she was unlikely to follow the subordinate's *static* gaze (peak at time= -7; $r = -0.1719$, $n = 416$; $-\log\text{-likelihood} = 8.6115$, $p < 0.05$).

In contrast, the subordinate followed the dominant's *static* gaze before she *approached* the dominant, but not after (Figure 6.56).

Cross Correlation, Pair 2 Competition: When the Subordinate Approaches the Dominant, Does the Subordinate Follow the Dominant's *Static* Gaze?

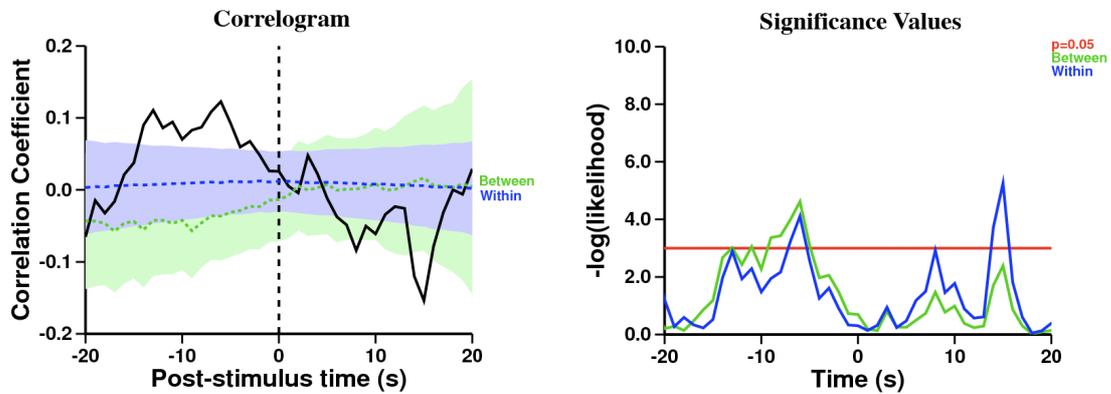


FIGURE 6.56: Referent behaviour: subordinate *approaching* the dominant/ Target behaviour: subordinate following the dominant's *static* gaze. After the subordinate walked towards the dominant from a different quadrant, she looked at the dominant and then both chimpanzees gazed towards the same direction significantly less than expected from the within-trial shuffled control (peak at time= +15, $r = -0.1539$, $n = 225$; $-\log\text{-likelihood} = 5.2574$, $p < 0.05$). The subordinate followed the dominant's *static* gaze before she *approached* the dominant (peak at time= - 6; $r = 0.1227$, $n = 436$; $-\log\text{-likelihood} = 4.1074$, $p < 0.05$).

Though overall during the *Competition* the dominant did not follow the subordinate's gaze onset, she did when she *approached* the subordinate (Figure 6.57).

Cross Correlation, Pair 2 *Competition*: When the Dominant Approaches the Subordinate, Does the Dominant Follow the Subordinate's Gaze Onset?

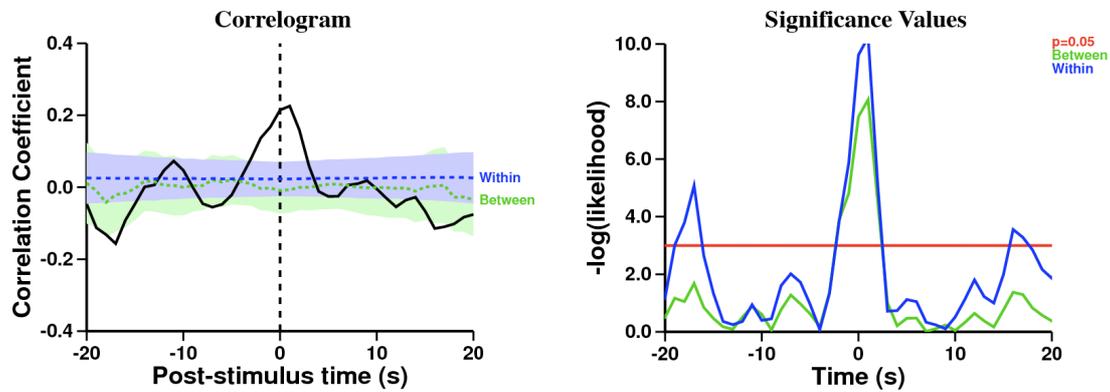


FIGURE 6.57: Referent behaviour: dominant *approaching* the subordinate. Target behaviour: dominant following the subordinate's gaze onset. After the dominant walked towards the subordinate from a different quadrant, the subordinate changed her gaze direction in view of the dominant and both chimpanzees gazed towards the same quadrant significantly more than expected from the within-trial shuffled control (peak at time= +1, $r = 0.2255$, $n = 565$; $-\log\text{-likelihood} = 10.2384$, $p < 0.05$). Before and long after the dominant *approached*, she was unlikely to follow the subordinate's gaze onset (peak at time= -17, $r = -0.1559$, $n = 192$; $-\log\text{-likelihood} = 5.0753$, $p < 0.05$. Peak at time= +16, $r = -0.1148$, $n = 228$; $-\log\text{-likelihood} = 3.5544$, $p < 0.05$).

The subordinate followed the dominant's gaze *onset* before she followed the dominant by *approaching* her (Figure 6.58). After the subordinate *approached* the dominant, she was significantly unlikely to follow the dominant's gaze *onset*.

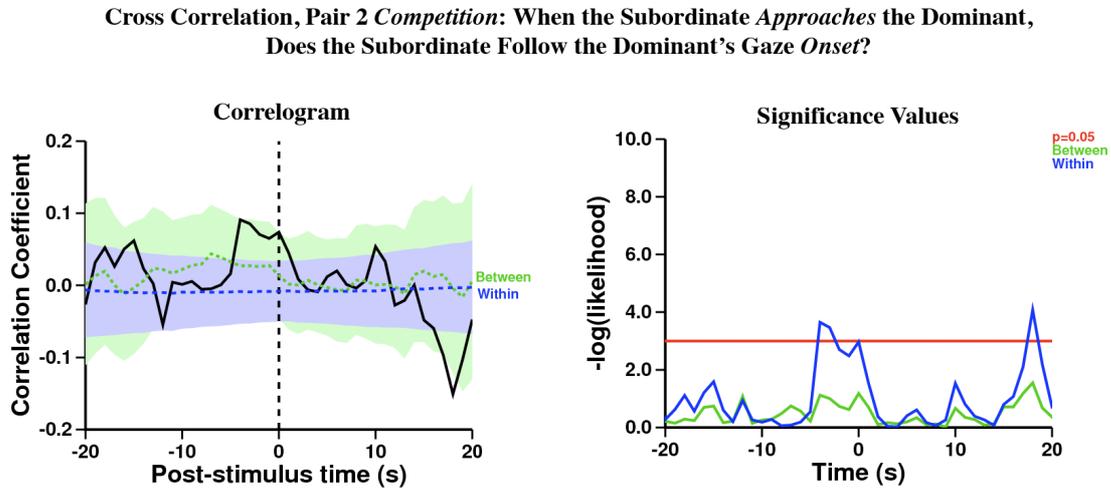


FIGURE 6.58: Referent behaviour: subordinate *approaching* the dominant. Target behaviour: subordinate following the dominant's gaze *onset*. Before the subordinate walked towards the dominant from a different quadrant, the dominant changed her gaze direction in view of the subordinate and then both chimpanzees gazed towards the same quadrant significantly more than expected from the within-trial shuffled control (peak at time= -4, $r=0.0910$, $n=473$; $-\log\text{-likelihood}=3.6494$, $p<0.05$). After the subordinate *approached*, she did not follow the dominant's gaze *onset* (peak at time= +18, $r=-0.1509$, $n=202$; $-\log\text{-likelihood}=4.0797$, $p<0.05$).

When the dominant *approached* the subordinate, she followed the subordinate's *static* gaze as well as her gaze *onset*, indicating that the dominant noticed changes in the subordinate's gaze, and may have used these as cues while *approaching* the subordinate. The subordinate followed the dominant's gaze using both gaze types before she *approached* the dominant, which suggests that the subordinate used gaze information to alter her movement towards the dominant.

Recall that when the dominant *approached* the subordinate, the subordinate was highly likely to stop walking altogether (see Chapter 5: Movement Following), possibly in order to avoid meeting the dominant near the food, or to avoid giving movement cues that the dominant could use in searching for the food. After the subordinate stopped walking, she was significantly likely to stop gazing in the direction of the bait as well ("Stop Gazing" was defined as a change from "Gazing towards the bait" to five consecutive seconds of "Not gazing towards the bait") (Figure 6.59).

**Cross Correlation, Pair 2 Competition: When the Subordinate Stops Walking,
Does she Stop Gazing Towards the Bait?**

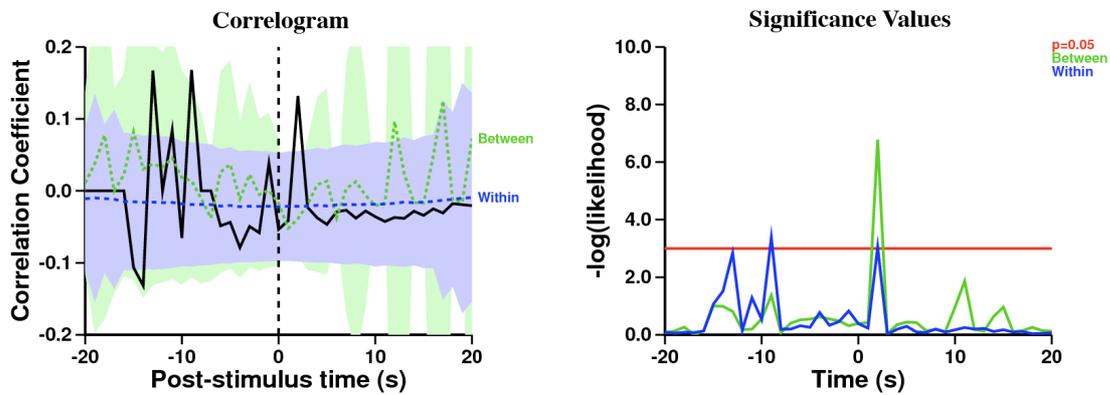


FIGURE 6.59: Referent behaviour: subordinate stops walking. Target behaviour: subordinate stops gazing towards the bait. After the subordinate stops walking for five seconds, she stopped gazing towards the bait for five seconds (peak at time= +2, $r = 0.1319$, $n = 144$; $-\log\text{-likelihood} = 3.0490$, $p < 0.05$). Before the subordinate stops walking, she stops gazing towards the bait significantly more than expected from the within-trial shuffled control (peak at time= -9, $r = 0.1681$, $n = 62$; $-\log\text{-likelihood} = 3.3775$, $p < 0.05$).

The subordinate's pause in movement as well as gaze demonstrates that she was able to withhold both physical and visual information about the location of the hidden bait from her dominant competitor.

2. Footsteps

I asked, "When the dominant follows in the subordinate's *footsteps*, does the dominant follow the subordinate's gaze (*static/onset*)?" The dominant's *static* gaze following alternates in a similar manner to her movement while following in the subordinate's *footsteps* (see Chapter 5: Movement Following): the dominant did, then did not, and again did follow the subordinate's *static* gaze (Figure 6.60). It is possible that movement and gaze are not independent effects. In contrast, there was no relationship of the subordinate following the dominant's *static* gaze while following in her *footsteps* (Figure 5.61). She followed the dominant's gaze long before following her movement, though this may be an artefact of the experimental setup.

Cross Correlation, Pair 2 Competition: When the Dominant Follows in the Subordinate's *Footsteps*, Does the Dominant Follow the Subordinate's *Static Gaze*?

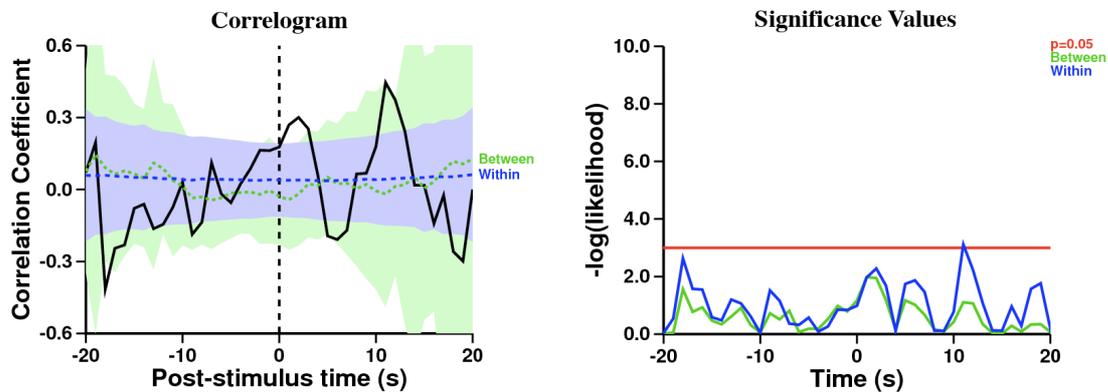


FIGURE 6.60: Referent behaviour: dominant following in the subordinate's *footsteps*. Target behaviour: dominant following the subordinate's *static gaze*. After the dominant was in the same quadrant and walking towards the same quadrant as the subordinate (and the dominant walking towards the subordinate and the subordinate away from the dominant), the dominant looked at the subordinate and then both chimpanzees gazed towards the same quadrant; this relationship trends towards being more than expected from the within-trial shuffled control (peak at time= +2, $r= 0.3006$, $n= 54$; $-\log\text{-likelihood}= 2.2793$, *ns*). After, the relationship trends towards being less than expected from the within-trial shuffled control (peak at time= +6, $r= -0.2087$, $n= 40$; $-\log\text{-likelihood}= 1.8672$, *ns*), and then again the relationship trends towards being more than expected (peak at time= +11, $r= 0.4459$, $n= 32$; $-\log\text{-likelihood}= 3.1122$, $p<0.05$).

Cross Correlation, Pair 2 Competition: When the Subordinate Follows in the Dominant's *Footsteps*, Does the Subordinate Follow the Dominant's *Static* Gaze?

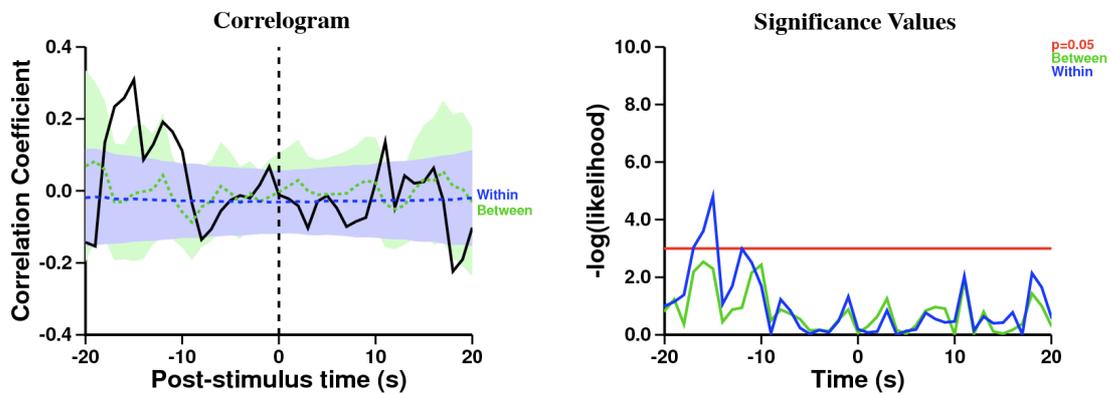


FIGURE 6.61: Referent behaviour: subordinate following in the dominant's *footsteps*. Target behaviour: subordinate following the dominant's *static* gaze. Before the subordinate was in the same quadrant and walking towards the same quadrant as the dominant (and the subordinate walking towards the dominant and the dominant away from the subordinate), she looked at the dominant and then both chimpanzees gazed towards the same quadrant (peak at time= -15, $r= 0.3090$, $n= 41$; $-\log\text{-likelihood}= 4.8088$, $p<0.05$), but after she followed in the dominant's *footsteps*, there was no relationship of the subordinate following the dominant's *static* gaze.

After the dominant walked in the subordinate's *footsteps*, there was no significant relationship of following the subordinate's gaze *onset* (Figure 6.62).

Cross Correlation, Pair 2 Competition: When the Dominant Follows in the Subordinate's Footsteps, Does the Dominant Follow the Subordinate's Gaze Onset?

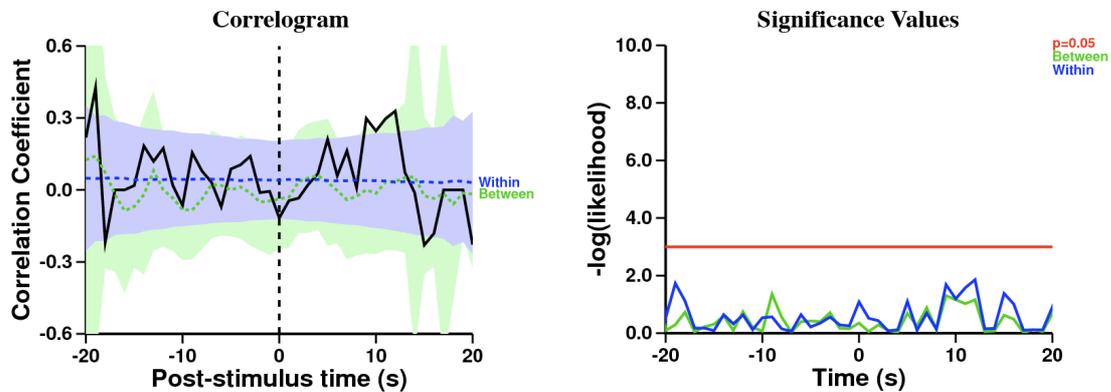


FIGURE 6.62: Referent behaviour: dominant following in the subordinate's *footsteps*. Target behaviour: dominant following the subordinate's gaze *onset*. There is no significant relationship between the two variables. After the dominant was in the same quadrant and walking towards the same quadrant as the subordinate (and the dominant walking towards the subordinate and the subordinate away from the dominant), the subordinate changed her gaze direction in view of the subordinate and then both chimpanzees gazed towards the same quadrant; this relationship trends towards being more than expected from the within-trial shuffled control (peak at time= +12, $r = 0.3287$, $n = 27$; $-\log\text{-likelihood} = 1.8558$, *ns*).

Before the subordinate walked in the dominant's *footsteps* she followed the dominant's gaze *onset* (Figure 6.63).

Cross Correlation, Pair 2 Competition: When the Subordinate Follows in the Dominant's *Footsteps*, Does the Subordinate Follow the Dominant's Gaze *Onset*?

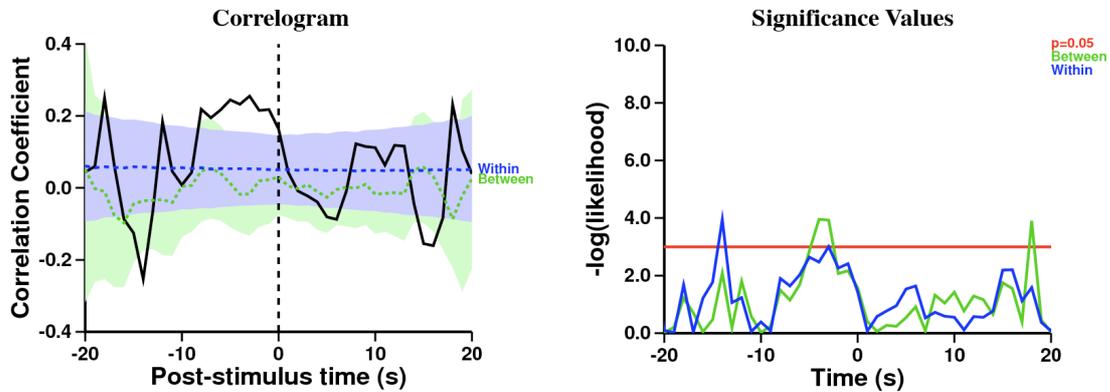


FIGURE 6.63: Referent behaviour: subordinate following in the dominant's *footsteps*. Target behaviour: subordinate following the dominant's gaze *onset*. Before the subordinate was in the same quadrant and walking towards the same quadrant as the dominant (and the subordinate walking towards the dominant and the dominant away from the subordinate), the dominant changed her gaze direction in view of the subordinate and then both chimpanzees gazed towards the same quadrant (peak at time= - 3, $r = 0.2550$, $n = 125$; $-\log\text{-likelihood} = 3.0068$, $p < 0.05$). Before, the relationship was significantly less than expected from the within-trial shuffled control (peak at time= -14, $r = -0.2539$, $n = 41$; $-\log\text{-likelihood} = 3.9482$, $p < 0.05$).

When the dominant followed in the subordinate's *footsteps*, she followed the subordinate's *static* gaze, but not her gaze *onset*. On the other hand, the subordinate did not follow the dominant's *static* gaze, but did follow her gaze *onset* before following in the dominant's *footsteps*.

3. Incongruent Gaze and Body Direction

I analysed whether changes in body direction were related to incongruent gaze and body direction. The subordinate changed her body direction before gazing towards a different direction, which gives the impression that she turned her body before her head (Figure 6.64).

Cross Correlation, Pair 2 Competition: When the Subordinate's Gaze and Body Direction are Incongruent, Does the Subordinate Change Body Direction?

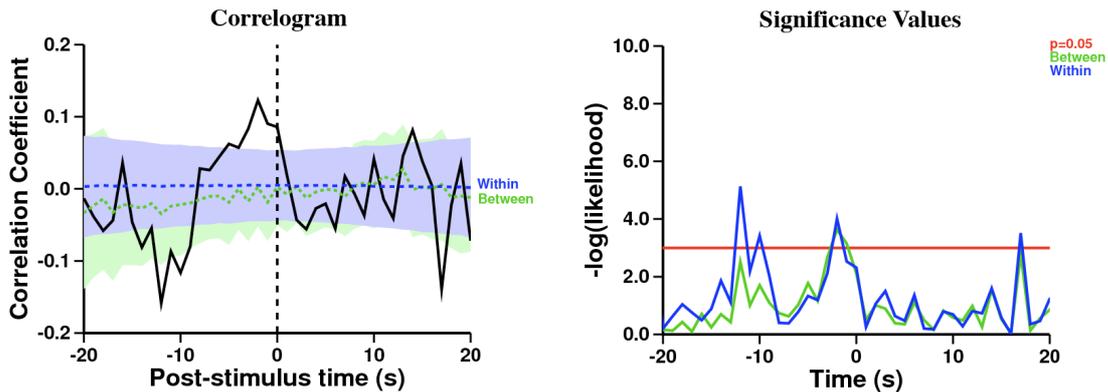


FIGURE 6.64: Referent behaviour: subordinate's gaze and body direction are incongruent. Target behaviour: subordinate changing her body direction. Before the subordinate's body and gaze were oriented towards different quadrants, she changed her body direction (peak at time = -2, $r = 0.1229$, $n = 475$; $-\log\text{-likelihood} = 4.0129$, $p < 0.05$). Before and after, the relationship is significantly less than expected from the within-trial shuffled control (peak at time = -12, $r = -0.1587$, $n = 270$; $-\log\text{-likelihood} = 5.1334$, $p < 0.05$. Peak at time = +17, $r = -0.1397$, $n = 228$; $-\log\text{-likelihood} = 3.5132$, $p < 0.05$).

An additional question concerns whether the dominant noticed when the subordinate gazed towards one quadrant while walking towards a different quadrant, which may give away the location of the hidden food. When the subordinate's gaze and body direction were incongruent, the dominant followed the subordinate's gaze *onset* eight seconds later, significantly more than expected from the within-trial shuffled control, though this may not be an ecologically valid relationship (Figure 6.65).

Cross Correlation, Pair 2 Competition: When the Subordinate's Gaze and Body Direction are Incongruent, Does the Dominant Follow the Subordinate's Gaze Onset?

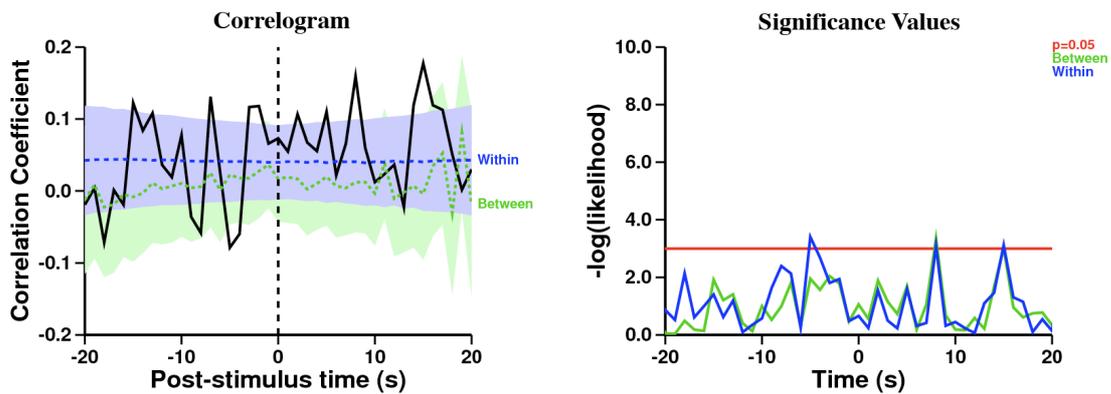


FIGURE 6.65: Referent behaviour: subordinate's gaze and body direction are incongruent. Target behaviour: dominant follows the subordinate's gaze *onset*. After the subordinate gazes towards one quadrant while walking towards another, the dominant followed the subordinate's change in gaze direction (peak at time= +8, $r = 0.1594$, $n = 314$; $-\log$ -likelihood= 3.0910, $p < 0.05$).

The dominant was unlikely to change her body direction after her gaze was incongruent with her body direction (Figure 6.66).

Cross Correlation, Pair 2 Competition: When the Dominant's Gaze and Body Direction are Incongruent, Does the Dominant Change Body Direction?

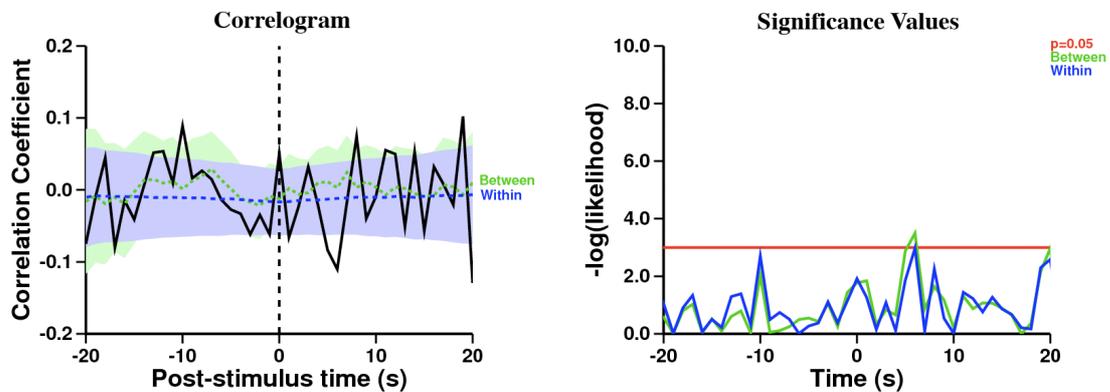


FIGURE 6.66: Referent behaviour: dominant's gaze and body direction are incongruent. Target behaviour: dominant changing her body direction. After the dominant's gaze and body were oriented towards different quadrants, the dominant did not change her body direction (peak at time= +6, $r = -0.1103$, $n = 440$; $-\log\text{-likelihood} = 2.9746$, *ns*).

Though the dominant was unlikely to change her direction of movement after her gaze and body were incongruent, the subordinate did notice the incongruity and was likely to follow the dominant's change in gaze direction (Figure 6.67).

Cross Correlation, Pair 2 Competition: When the Dominant's Gaze and Body Direction are Incongruent, Does the Subordinate Follow the Dominant's Gaze Onset?

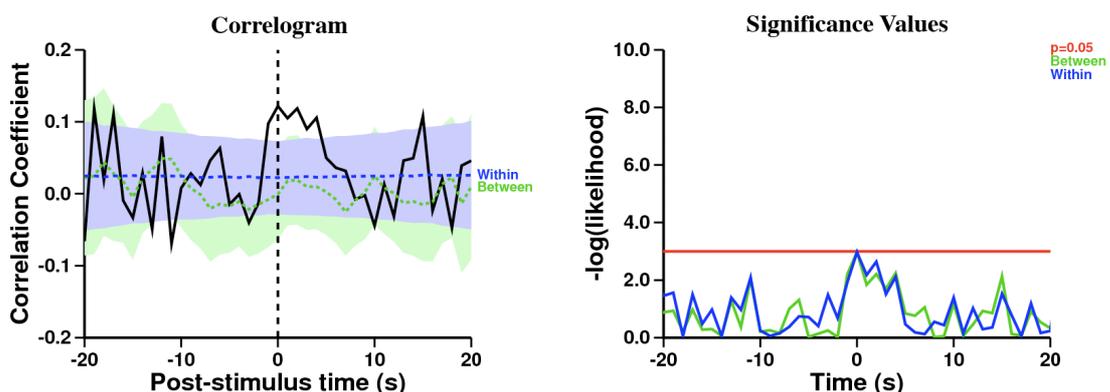


FIGURE 6.67: Referent behaviour: dominant's gaze and body direction are incongruent. Target behaviour: subordinate follows the dominant's gaze onset. After the dominant gazes towards one quadrant while walking towards another, the subordinate follows the dominant's change in gaze direction (peak at time= +0, $r = 0.1218$, $n = 416$; $-\log\text{-likelihood} = 2.9705$, *ns*).

The subordinate changed her body direction before it became incongruent with her gaze direction, and the dominant only followed the subordinate's change in gaze direction several seconds after the change. The dominant did not change her body direction at all after her gaze and body direction were incongruent, but the subordinate did follow the dominant's gaze change.

4. Convergence

When both chimpanzees were in different quadrants and walking towards the same quadrant, both chimpanzees were likely to be following the other's *static* gaze by first looking at her opponent and then looking towards their destination (Figures 6.68 and 6.69).

Cross Correlation, Pair 2 Competition: When Both Chimpanzees Converge, Does the Dominant Follow the Subordinate's Static Gaze?

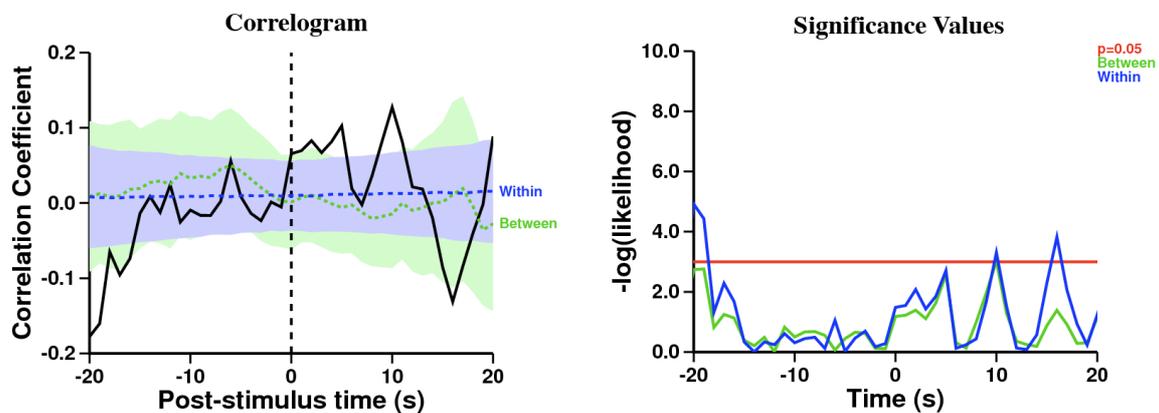


FIGURE 6.68: Referent behaviour: both chimpanzees *converging*. Target behaviour: dominant following the subordinate's *static* gaze. After both chimpanzees were in different quadrants and walking towards the same quadrant, the dominant looked at the subordinate and then both chimpanzees gazed towards the same quadrant (time= +5, $r = 0.1026$, $n = 494$; $-\log\text{-likelihood} = 2.7052$, *ns*. Peak at time= +10, $r = 0.1273$, $n = 372$; $-\log\text{-likelihood} = 3.3059$, $p < 0.05$). Later, the dominant did not follow the subordinate's *static* gaze (peak at time= +16, $r = -0.1313$, $n = 237$; $-\log\text{-likelihood} = 3.8235$, $p < 0.05$). Before the chimpanzees *converged*, the dominant did not follow the subordinate's *static* gaze (peak at time= -20, $r = -0.1777$, $n = 169$; $-\log\text{-likelihood} = 4.9175$, $p < 0.05$).

**Cross Correlation, Pair 2 *Competition*: When Both Chimpanzees Converge,
Does the Subordinate Follow the Dominant's *Static* Gaze?**

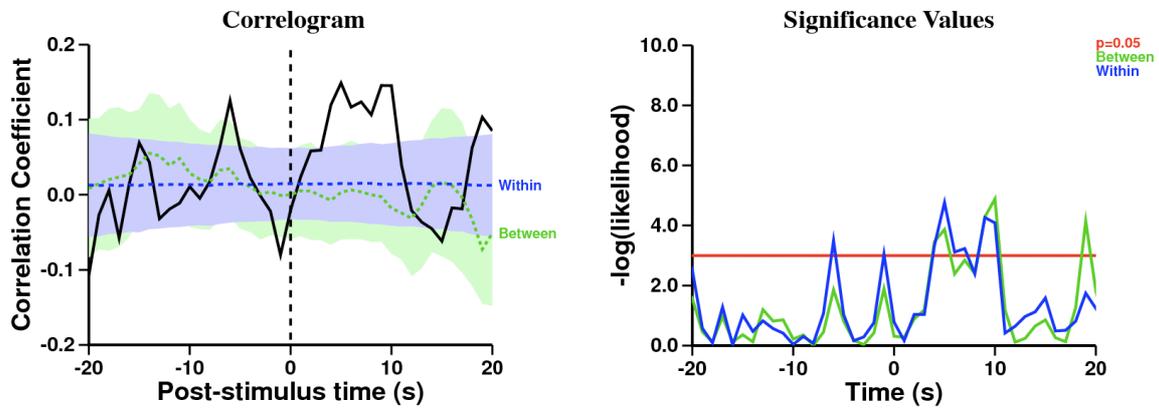


FIGURE 6.69: Referent behaviour: both chimpanzees *converging*. Target behaviour: subordinate following the dominant's *static* gaze. After both chimpanzees were in different quadrants and walking towards the same quadrant, the subordinate looked at the dominant and then both chimpanzees gazed towards the same quadrant (peak at time= +5, $r = 0.1489$, $n = 492$; $-\log\text{-likelihood} = 4.7642$, $p < 0.05$). The subordinate appeared to alternate between following the dominant's *static* gaze and not following, before the chimpanzees *converged* (peak at time= -6, $r = 0.1254$, $n = 436$; $-\log\text{-likelihood} = 3.4980$, $p < 0.05$. Peak at time= -1, $r = -0.0803$, $n = 561$; $-\log\text{-likelihood} = 3.0402$, $p < 0.05$).

However, there is no significant relationship of either subject following the other's gaze onset while *converging* (Figures 6.70 and 6.71). After the chimpanzees *converged*, it appears that the dominant at first did not follow the subordinate's gaze onset, but then did several seconds later, though this relationship is not significant. In the same time frame, the pattern in the correlogram shows that the subordinate did not follow the dominant's gaze onset.

Cross Correlation, Pair 2 Competition: When Both Chimpanzees Converge, Does the Dominant Follow the Subordinate's Gaze Onset?

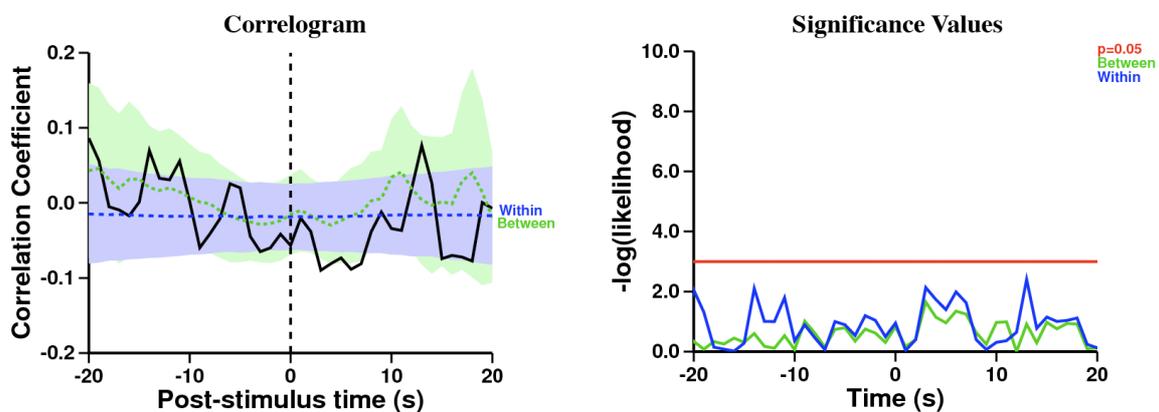


FIGURE 6.70: Referent behaviour: both chimpanzees *converging*. Target behaviour: dominant following the subordinate's gaze onset. After both chimpanzees were in different quadrants and walking towards the same quadrant, the subordinate changed her gaze direction in view of the dominant and then both chimpanzees gazed towards the same quadrant; this relationship trends towards being less than expected from the within-trial shuffled control (peak at time= +3, $r = -0.0898$, $n = 536$, $-\log\text{-likelihood} = 2.1323$, *ns*). Later, this relationship trends towards being more than expected from the within-trial shuffled control (peak at time= +13, $r = 0.0764$, $n = 290$; $-\log\text{-likelihood} = 2.4048$, *ns*).

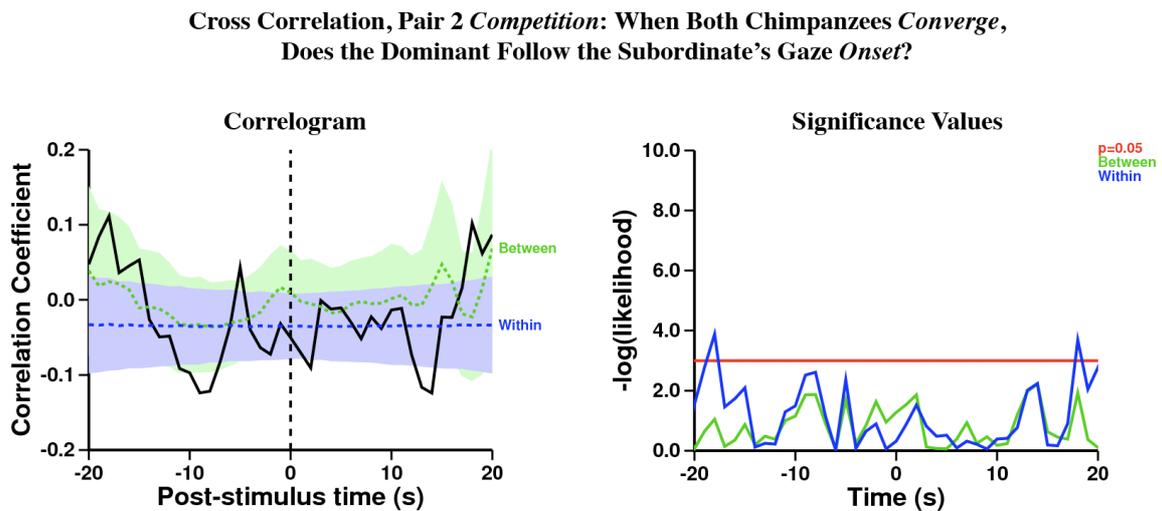


FIGURE 6.71: Referent behaviour: both chimpanzees *converging*. Target behaviour: dominant following the subordinate's gaze *onset*. Before both chimpanzees were in different quadrants and walking towards the same quadrant, the subordinate changed her gaze direction in view of the dominant and then both chimpanzees gazed towards the same quadrant; this relationship alternates between trending towards being more than, and less than expected from the within-trial shuffled control (Peak at time= -18, $r = 0.1116$, $n = 187$; $-\log\text{-likelihood} = 3.8830$, $p < 0.05$. Time= -8, $r = -0.1217$, $n = 383$; $-\log\text{-likelihood} = 2.6131$, *ns*. Time= -5, $r = 0.0433$, $n = 448$; $-\log\text{-likelihood} = 2.3642$, *ns*). After the chimpanzees *converged*, the dominant continued to alternate: she did not follow the subordinate's gaze *onset* (time= +14, $r = -0.1242$, $n = 274$; $-\log\text{-likelihood} = 2.2375$, *ns*), and then she did (time= +18, $r = 0.1021$, $n = 202$; $-\log\text{-likelihood} = 3.6907$, $0 < 0.05$).

When both chimpanzees *converged*, they both followed their opponent's *static* gaze but only the dominant appeared to follow the subordinate's gaze *onset*. Though in the overall *Competition* the dominant did not follow the subordinate's gaze *onset*, she did when she *converged* on the subordinate's movement.

5. Summary

The dominant followed the subordinate's *static* gaze when she used the three defined movement types. The subordinate followed the dominant's *static* gaze before she *approached* the dominant, and to monitor the dominant while both chimpanzees *converged*, but not when she walked in the dominant's *footsteps*. The dominant's *static* gaze following temporarily coincided with her movement following: gaze follows occurred at the moment or shortly after a movement follow was initiated, which implies that for the dominant, physical movement following led to an increase in gaze following. However, the subordinate usually followed the dominant's *static* gaze, and gaze *onset*, before she followed the dominant's

movement, indicating that for her, gaze following led to movement following; this makes Reinette different from the other subjects in the study. The dominant of this pair, Georgia, was constantly moving through the enclosure, and as described in Chapter 5: Movement Following, the dominant often “followed from in front,” by surpassing the subordinate on her path. The subordinate was looking directly at the dominant for a large percent of time that her gaze was recorded (43.92%, compared to the dominant looking at the subordinate 23.33% of the time her gaze was recorded), and so it could be the case that the subordinate looked at the dominant, then followed the dominant’s gaze (and body) as the dominant passed in front of her to the leader position. This explanation helps to put into the context of the interaction a possible reason that the subordinate followed gaze before following movement. Additionally, when the subordinate started to walk in a different direction, she kept an eye on the dominant to gauge whether the dominant was paying attention to her, which explains why the subordinate changed her body direction before her body and gaze were incongruent (whereas for the chimpanzees of Pair 1, both subjects’ gaze was incongruent with their body direction before they changed their body direction, indicating that they first looked towards a direction before turning towards it).

Whereas the dominant only followed the subordinate’s gaze *onset* while *approaching* her, the subordinate followed the dominant’s gaze *onset* both before *approaching* and before following in her *footsteps*. The correlograms depicting the dominant’s movement while following in the subordinate’s *footsteps* showed that she alternated between the follower and leader positions (see Chapter 5), and her gaze behaviour appears to adhere to the same pattern: when the dominant followed in the subordinate’s *footsteps*, she alternated between following the subordinate’s *static* gaze and gazing towards other locations.

VI. Overall Summary of Pair 2, Reinette and Georgia

I examined two types of gaze behaviour: *static* gaze following and following gaze *onset* (Table 6.6 summarises the result of each gaze analysis for each experimental condition).

TABLE 6.6: Overall summary of different gaze following types throughout the experiment, Pair 2 (Results listed in Prediction/Outcome format)

	Overall <i>Competition</i>	<i>No Knowledge</i>	<i>Full Knowledge</i>	<i>No Bait, No Knowledge</i>
Dominant follows Subordinate's <i>static gaze</i>	Yes/Yes	No/Yes	No/No	No/Yes
Subordinate follows Dominant's <i>static gaze</i>	No/No	No/Yes	No/Yes	No/No
Dominant follows Subordinate's <i>gaze onset</i>	Yes/No	No/No	No/Yes	No/No
Subordinate follows Dominant's <i>gaze onset</i>	No/No	No/No	No/No	No/No

The dominant followed the subordinate's *static gaze* in every condition except when she had seen where the bait was hidden: during the *Full Knowledge* controls the dominant did not follow the subordinate's *static gaze*. The subordinate did not follow the dominant's *static gaze* when she had privileged information regarding the location of the hidden bait. The subordinate did follow *static gaze* during the controls, but her failure to follow the dominant's gaze during the *No Bait, No Knowledge* trials raises the question as to how reliable negative results are. Perhaps the subordinate did not follow the dominant's gaze because it had never been rewarding for her: she had privileged information during the *Competition* and was successful in finding food without following gaze, and on the *No Knowledge* and *Full Knowledge* controls, when she did follow the dominant's gaze, the dominant picked up the bait. Additionally, the subordinate spent more time not moving at all during the *No Bait, No Knowledge* controls (see Chapter 5) and may not have been motivated to follow the dominant's gaze while not physically following.

The subjects of Pair 2 used *gaze onset* cues when not in close proximity. For example, the dominant followed the subordinate's *gaze onset* (as well as *static gaze*) when *approaching* her from a different quadrant. The subordinate rarely *approached* the dominant,

but when she did, she stopped shortly after; when the subordinate stopped moving, she also stopped gazing towards the bait, effectively withholding both movement and gaze cues from the dominant. The subordinate may have acted in this way simply to avoid meeting the dominant near the food, but her actions functioned to deceive the dominant in these instances, and this behaviour can be considered an example of tactical deception (Byrne & Whiten, 1988).

VII. Gaze Following Discussion for Both Pairs

My analysis using cross correlations aimed to elucidate how chimpanzees used two different types of gaze following during the informed forager paradigm. In general, I aimed to show how the dominant was able to obtain information from the subordinate regarding the location of the hidden food, and what information the subordinate could use to change her tactic by following the dominant's gaze. In particular, I analysed whether each subject followed the other's gaze when it was *static* or dynamic, i.e., a gaze *onset*, and how these two types related to three different movement following types (described in full in Chapter 5).

For both pairs, the dominant followed the subordinate's *static* gaze when the dominant did not know where the bait was hidden in the *Competition* and *No Knowledge* controls, whereas the subordinate did not follow the dominant's *static* gaze when she had privileged knowledge of the location of the hidden food. This pattern was reversed for both pairs during the *Full Knowledge* controls: the subordinate followed the dominant's *static* gaze, but the dominant did not follow the subordinate's.

However, the chimpanzees' use of following gaze *onset* was different between individuals. In Pair 1, the subordinate Missy followed the dominant Rita's gaze *onset* in every condition; in Pair 2, the exact opposite result was found: the subordinate Reinette did not follow the dominant Georgia's gaze *onset* in any condition. In Pair 1, the dominant only followed the subordinate's gaze *onset* during the *Competition* and *No Bait, No Knowledge* trials. In Pair 2, the dominant followed the subordinate's gaze *onset* only in the *Full Knowledge* trials.

When gaze types were analysed in relation to different types of movement following, similarities and differences emerged between the two pairs. Both dominants followed the subordinates' *static* gaze while *approaching*, following in her opponent's *footsteps*, and *converging*. None of the four subjects followed her opponent's gaze *onset* while *converging*.

The subjects of Pair 1 followed the other's gaze *onset* while following in her *footsteps*, whereas both from Pair 2 followed the other's gaze *onset* when not yet in close proximity while *approaching*—the subordinate followed the dominant's gaze *onset* (and *static gaze*) before *approaching* her.

In contrast to Pair 1 in which both subjects followed the other's gaze using both types while following in her *footsteps*, the subordinate of Pair 2 only followed the dominant's gaze *onset* before following in her *footsteps*, and did not follow her *static gaze* at all, and the dominant did not follow the subordinate's gaze *onset*.

The subordinates differed in their following of the dominants' gaze: the subordinate of Pair 1 followed the dominant's gaze using both types while following in her *footsteps*, but the subordinate of Pair 2 only followed the dominant's gaze *onset* before following in her *footsteps*. Furthermore, the subordinate of Pair 1 did not follow the dominant's gaze using either type while *converging*, but the subordinate of Pair 2 did follow her competitor's *static gaze*.

Unlike the results from Pair 1 for which an incongruent direction of body and gaze preceded a change in body direction for both subjects, in Pair 2, the subordinate changed her body direction before it became incongruent with her gaze direction, and the dominant did not change her body direction at all. Yet all four subjects followed her opponent's gaze *onset* when her gaze was incongruent with her direction of movement.

This study provides detailed evidence that chimpanzees follow conspecific gaze in a naturalistic foraging scenario, and the strongest experimental evidence thus far that they use visual information to modify their competitive tactics. While previous naturalistic studies reported that subjects appeared to use conspecific gaze cues (Menzel, 1974; Coussi-Korbel, 1994; Held et al., 2000, 2002, 2010; Hare et al., 2001, 2003; Hirata & Matsuzawa, 2001; Ducoing & Thierry, 2003, 2004; Bugnyar & Kotrschal, 2004; Schloegl et al., 2008b), and experimental studies have concluded that chimpanzees “know what conspecifics do and do not see,” and furthermore that they “know what conspecifics know” (Hare et al., 2000, 2001), none of these studies has specifically addressed how gaze is utilized to gain information from a competitor nor how that information is used to change one's own competitive tactic. My study specifically analyses the use and influence of gaze: the result that chimpanzees can use conspecific gaze cues in an ecologically valid competitive context contrasts with previous studies in which chimpanzees were unable to use a cooperative visual cue given by a human

demonstrator to find hidden food (Povinelli & Eddy, 1996; Povinelli et al., 1999). I present new evidence that shows how each subject follows the gaze and movement of her competitor, and how they use visual information to adjust their own movement either towards or away from the hidden bait.

Chance's social attention hypothesis (1967) predicted that subordinates look more at dominants than at similarly-ranked individuals, and that dominants look more at similarly-ranked individuals than at those subordinate to them (supporting evidence also published by McNelis & Boatright-Horowitz, 1998; Kaplan & Rogers, 2002; Shepherd et al., 2006). One would expect that all individuals are looking 'up' the dominance hierarchy to gain information from alphas regarding social interactions, the location of food or predators, and that the next logical step after looking to a dominant is to follow that individual's gaze in order to find such valuable visual information. Thus, a reasonable extension of the social attention hypothesis is that subordinates are more likely to follow the dominants' gaze than the dominants are to follow the subordinates' gaze (because dominants are not looking at subordinates). The pattern of *static* gaze following that I observed is the opposite of this prediction: though both subjects in Pair 1 looked directly at her opponent an approximately equal percent of the time that their gaze was recorded (28% and 32%), the cross correlations showed that the dominant followed the subordinate's *static* gaze and her gaze *onset* throughout the *Competition*, and the subordinate did not follow the dominant's *static* gaze; the subordinate did follow the dominant's gaze *onset*, especially when following in the dominant's *footsteps*. For Pair 2, the subordinate did look more to the dominant (44% vs. 23% of the time that their gaze was recorded), but the dominant followed the subordinate's *static* gaze more than the reverse, and neither followed the other's gaze *onset*.

Results linking the two gaze types with the three movement types support previous narrative reports in the informed forager paradigm that evoked the sense that the dominant used the subordinate's gaze cues to inform her search for the bait. Cross correlations confirm that each dominant did in fact use gaze information to alter her movement while *converging*: she looked at the subordinate and then geometrically matched her gaze towards the same quadrant as the subordinate's gaze direction (Tomasello et al., 1999), while readjusting her own movement to intersect the subordinate's path. Similarly, the dominants followed the subordinates' *static* gaze both before and during an *approach*, and in Pair 1 the dominant

picked up on subtle changes in the subordinate's gaze direction while following in her *footsteps*.

Analyses of how each subject followed gaze *onset* indicate that changes in gaze direction may be more noticeable in close proximity, and that noticing these cues is especially useful in these circumstances, as a change in gaze direction can precede a change in movement direction (Nummenmaa, et al., 2009). Being able to follow these gaze changes may help each subject to anticipate her opponent's next move—a critical ability during a competitive foraging interaction over limited resources. At greater distances, a change in movement direction may be a more salient cue during the search for a hidden item than a change in gaze direction (Shepherd, 2010). Furthermore, every subject noticed when her opponent's gaze direction was incongruent with her direction of movement, so the knowledgeable subordinate may have betrayed the location of the hidden food to the ignorant dominant by looking towards it while not walking towards it.

That the subordinate subjects were able to withhold gazing towards the bait during episodes in which the dominants were exploiting them raises the question of intent; their behaviour functioned to tactically deceive their opponents. Gómez (1991) and de Waal (2001) have discussed apes' use of deictic gaze: in both cases an ape subject established a communicative intent with a human tool and used gaze to intentionally modify what their human companion could see by drawing the researcher's attention to an out of reach goal. The behaviour observed in this experiment raises the question of whether similar gaze cues are intentionally withheld from competitors, as “eye gaze cues have long been assumed...to be a major nonverbal behaviour through which deceptive individuals may leak information about both deceptive intent and the truth” (Freire et al., 2004). It is possible that the subordinate chimpanzees in this study avoided gazing towards the bait in order to reduce their own anxiety over approaching it in the presence of the dominant, and a learning account would suggest that subordinates had learned that their opponent was likely to follow the trajectory of their movement and gaze towards the bait. A more cognitive interpretation would suggest that the subordinates countered the dominants' exploitation of visual cues by intentionally gazing in a different direction, thus acting to achieve their ultimate goal of picking up the food while the dominant was looking elsewhere. Gaze following is a precursor to human-like theory of mind, so acting to prevent gaze following towards a goal may

suggest that chimpanzees understand that their gaze direction can reveal their desires or intentions to other individuals.

The next chapter will address whether chimpanzees use gaze types differently while walking towards food rewards of different preference value (highly preferred banana or less preferred cucumber): whether gaze is used to recruit a competitor to a less-preferred bait, how often the subject ‘checks back’ to their competitor when walking towards the cucumber compared to the banana, and if gaze is withheld when approaching a more-preferred item.

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I. Abstract

In the first experiment, the *Competition* described in Chapters 5 and 6, dominant chimpanzees were able to follow subordinates' gaze in order to modify their own movement towards a goal, and subordinates were able to withhold their gaze towards the goal to prevent the dominants from scrounging. In the present chapter, I introduced two hidden rewards, a banana and a cucumber, on the hypothesis that the subordinate would treat the less preferred cucumber as a 'decoy,' and allow the dominant to scrounge on it while she was able to reach the preferred banana first. The idea was to explore whether and how the subordinates were able to use visual cues to attract competitors to a less valuable food reward. Specific behaviour was recorded: when the subordinate alternated her gaze between the dominant and either bait, i.e., a *monitoring* glance, and when the gaze was accompanied by a pause in locomotion, i.e., a *recruitment* glance. Whether the dominant approached the bait towards which the subordinate gazed was also recorded. Both subordinates *monitored* before walking towards the banana, and did not *recruit* towards the banana; one subordinate also *monitored* throughout her approach to the cucumber. One subordinate *recruited* her opponent towards the cucumber, pausing her movement towards the reward. The dominants followed towards hidden baits after the subordinates used either cue, but one subordinate's use of the *recruitment* cue towards only the cucumber suggests that her behaviour may have been an intentional manipulation of the dominant's behaviour: subordinate Reinette used the tactic to *recruit* dominant Georgia to the cucumber and subsequently left the area to retrieve the banana for herself. Her behaviour appeared to be an example of tactical deception by attraction: the subordinate used misleading tactics by moving towards an object of interest (the cucumber) which functioned to take the dominant's attention away from the subordinate's goal (the banana).

II. Introduction

Previous studies on collective movement in primates have shown that both vocal and visual communication play a role in determining whether other individuals follow a movement initiated by a leader (Boinski, 1993; Leca et al., 2003; Sueur & Petit, 2010). Yet under field conditions, visual communication may be very difficult to record (Boinski & Campbell, 1995; Meunier et al., 2008). In a naturalistic captive setting, white-faced capuchins (*Cebus capucinus*), tonkean and rhesus macaques (*Macaca tonkeana* and *M.*

mulatta) have been shown to use glances to recruit followers, and to monitor group-mates as they join the group of travellers (Leca et al., 2003; Meunier et al., 2008; Sueur & Petit, 2010). In all three studies, leaders relied more on visual cues than on vocal or other cues to initiate others to follow. In particular, leaders glanced back at group-mates to monitor the identity and number of followers, and leaders increased their speed and reduced the number of glances as the number of followers increased. Meunier et al. (2008) suggested that looking back to group-mates “seems to be an intentional behaviour of monitoring while its consequence is a recruitment of conspecifics” (Meunier et al., 2008, p.30). Additionally, Sueur and Petit (2010) determined that a leader’s pause in locomotion while glancing back to the group served as a recruitment cue for specific individuals, and was not due to uncertainty.

In Chapter 6, I found that the dominant chimpanzee in the informed forager *Competition* was able to use visual cues from the subordinate, in particular by following her gaze direction, in order to alter her physical movement towards the subordinate and/or the hidden bait. Furthermore, the subordinate was able to withhold her gaze towards the bait under the circumstance of heavy exploitation from the dominant, in the forms of physically close following and taking the bait. In order to further investigate visual cueing and tactical deception in the subordinate, I hid two rewards of different preference value, a banana and a cucumber, in the *Unequal Rewards* experiment presented here. After observing an escalating ‘arms race’ of tactics between two competing chimpanzees in his study, Menzel (1974) added a second, smaller food item near the original food pile, and noted that the informed subordinate led the dominant to the smaller piece first, and then ran to retrieve the larger pile for herself. In my previous experiment with one reward, the subordinates in both pairs had learned that their dominant partners exploited their foraging success by taking the food (Pair 1) or by running ahead of the subordinate’s path to search (Pair 2). In the *Unequal Rewards* experiment, with the same individual chimpanzees, if the subordinate treats the cucumber as a ‘decoy’ that the dominant might exploit, the subordinate should approach this piece of food first. My analysis addresses whether the subordinate used visual cues differently when walking towards a less preferred food item, and whether the dominant could pick up on those differences.

I distinguished two specific types of gaze: *monitoring* glances and *recruitment* glances. On the surface, both appear very similar: a subject alternates between looking at her opponent and gazing towards the hidden bait. A noticeable difference between the two types

of gaze, however, is that a subject employing *recruitment* glances will pause in her movement as she gazes towards her opponent (Sueur & Petit, 2010). I therefore defined *monitoring* glances as: “one subject looks at the other individual, and then gazes towards the bait for two seconds.” I defined *recruitment* glances as: “one subject looks at the other individual, and then gazes towards the bait for two seconds, and pauses in her locomotion for five seconds.” Thus, *recruitment* glances are a subset of *monitoring* glances. I hypothesised that the subordinate would use *recruitment* glances when walking towards the cucumber, and *monitoring* glances while walking towards the banana. Moreover, I hypothesised that the dominant should approach the subordinate more when she uses *recruitment* glances. These predictions are based on the assumption that the desired outcome of a *recruitment* glance, but not a *monitoring* glance, is for the opponent to walk towards the gazer and the destination. All experimental details were otherwise as described in Chapter 3.

III. Results: Pair 1

A. Results of Preference Test

Each subject was individually tested for her preference between banana and cucumber. Subordinate Missy chose banana 10 out of 10 times, and dominant Rita chose banana 9 out of 10 times.

B. Who Found the Rewards?

The subordinate, Missy, was informed of the location of a hidden banana and a hidden cucumber, always in that order, on the twenty *Unequal Reward* trials. Missy obtained a majority of the rewards: 15 bananas and 15 cucumbers (75% of total rewards); dominant competitor Rita found the remaining 5 bananas and 5 cucumbers (25%) (Figure 7.1). These percentages are the same as in the one reward *Competition* trials, indicating that Rita continued to exert moderate exploitation pressure upon Missy.

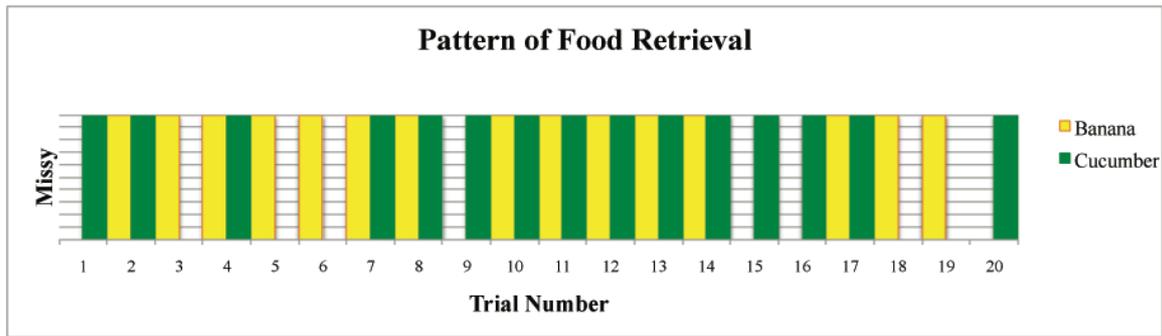


FIGURE 7.1: Pattern of the Subordinate's Food Retrieval, Pair 1

Rita picked up a banana on trials 1, 9, 15, 16, 20, and a cucumber on trials 3, 5, 6, 18, 19. Rita was first to pick up a reward on six trials. Overall, the average trial length was 58.4 seconds, and on average it took the chimpanzees 35.0 seconds to find the banana, and 45.0 seconds to find the cucumber. The subordinate approached the cucumber before the banana on eight trials.

Knowledgeable subordinate Missy did not pick up the bait that she first approached on two trials, because Rita picked it up. On trial 1, Missy found the banana in the small tire in Quadrant 4, but abandoned it and let Rita take it. On trial 9, Missy first approached the banana in the hammock in Quadrant 1, but Rita was physically closer where it was hidden, and when Rita turned to walk towards the hammock, Missy adjusted her direction to walk towards where the cucumber was hidden instead, and Rita found the banana. On nine trials, Missy first approached one bait, but changed her direction and picked up the other instead, before returning to the first. That the first bait approached was often the second to be retrieved indicates that the subordinate changed her direction on many trials, perhaps in response to the dominant's movement.

C. Descriptive Account of *Unequal Rewards*

On the first trial of the *Unequal Rewards* experiment, the knowledgeable subordinate walked directly to where the banana was hidden in the small tire in Quadrant 4, but then abandoned the location, allowing the dominant to take the bait. The subordinate walked away from the banana and towards the cucumber, and picked up the cucumber from the hammock in Quadrant 1 at around the same time that the dominant retrieved the banana. On the next four trials, the dominant searched in the small tire where the banana had been on trial one. On the second trial, the subordinate picked up both rewards and the dominant did not seem to pay attention. The dominant found a cucumber under the kegs in Quadrant 4 on the third trial,

and searched in the same location on the next trial as well. On the fourth trial, the subordinate looked over her shoulder to check on the dominant before she picked up the banana at the culvert in Q1, and then retrieved the cucumber from under the red ring in Q4 after the dominant had returned inside. The dominant continued to search where the banana was hidden on trial one, and then on trial six she stopped searching in the former location and instead searched the hanging tire in Q3 where the subordinate uncovered the banana on trial five.

The dominant followed the subordinate closely on trials six and seven, and threatened the subordinate on trial seven. The subordinate was careful to look back at the dominant before picking up both of the rewards on that trial, and the dominant peered as the subordinate ate the cucumber. The subordinate picked up both baits again on the next trial. On trial nine, the dominant searched under the kegs in Q3 where the subordinate had found the cucumber on the previous trial. Then, as the dominant walked towards the subordinate uncovering the cucumber in Q4, the dominant came across the banana in the hammock of Q1. On trial ten, the dominant searched several locations throughout quadrants 1 and 3, including the location where the subordinate had found the cucumber on that trial; both chimpanzees returned inside and several minutes later the subordinate re-entered the enclosure and picked up the banana from under the red ring in Q3.

On trial 11, the dominant walked past where the cucumber was hidden and then the subordinate picked it up. The dominant *approached* the subordinate and threatened her, then searched in the same location at the culvert in Q3. The dominant then followed as the subordinate began searching for the banana under the kegs in Q4. While the subordinate sat eating both of the food items, the dominant peered and picked up scraps of the cucumber that the subordinate passively allowed her to take. On the next trial, the subordinate ran to retrieve both rewards and the dominant followed, and the dominant again peered as the subordinate ate. On trial 14, the dominant walked towards Q1 and came very close to where the cucumber was hidden, without searching or finding it; the subordinate meanwhile had retrieved the banana in Q2, and walked to the central climbing structure. The dominant *converged* on the subordinate's movement and also sat on the structure, and then watched as the subordinate walked to where she had been standing in Q1, and the subordinate found the cucumber in the tire there. The dominant found the banana on the next trial under the kegs in Q3, and then searched in that same location on two trials afterward.

On trial 17, the dominant searched where the banana had been on trial 15, and the subordinate found the banana elsewhere. The dominant *approached* the subordinate and stopped to search in the hammock in Q1, but did not uncover anything; as the dominant climbed up onto the structure, the subordinate picked the cucumber from the hammock. The dominant found the cucumber on the next two trials and the subordinate picked up the bananas. On the final trial, the subordinate got the cucumber and then the dominant found the banana.

When the dominant did find a reward, it appeared on many trials that she came across a bait by searching familiar locations; however, she did continue to follow the subordinate's movement and gaze which may suggest that she continued to use those cues while searching for hidden foods (Correlograms with *approach*, *footsteps*, *convergence*, and *static gaze* are included in the appendix to Chapter 7).

D. Analysis of Walking Towards the Two Baits

I used cross correlations to address the subjects' movement towards the two hidden baits, banana and cucumber. Only the subordinate had seen where the two food items were hidden on each trial, and since previous analyses for this pair showed that the dominant walked towards the banana only after the subordinate walked towards it (See Chapter 5: Movement Following), I again asked, "When the subordinate walks towards the banana, does the dominant walk towards the banana?" and also, "When the subordinate walks towards the cucumber, does the dominant walk towards the cucumber?"

The cross correlation in Figure 7.2 shows that only after the subordinate started walking towards the banana did the dominant walk towards it, but not before. Data are compared to the within-trial shuffled control; this particular control is used because the bait is in a different location on each trial.

Cross Correlation, Pair 1 Unequal Rewards: When the Subordinate Walks Towards the Banana, Does the Dominant Walk Towards the Banana?

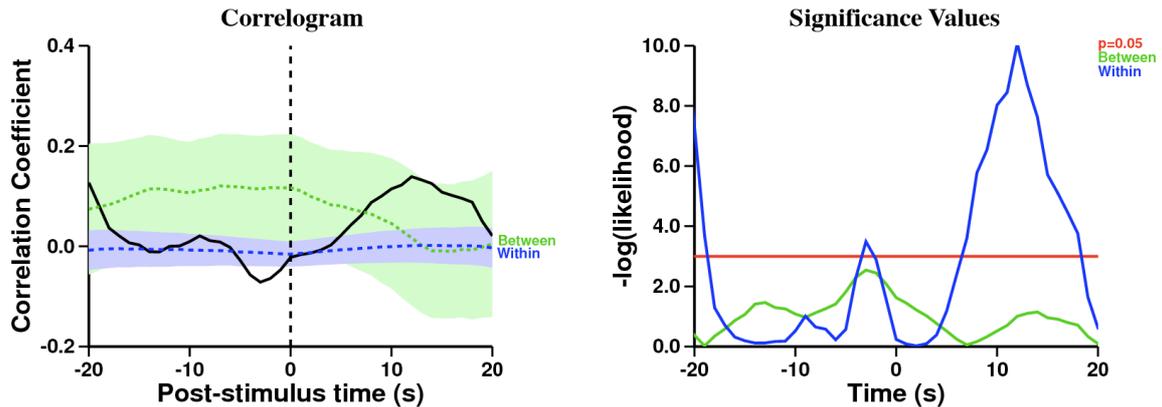


FIGURE 7.2: Referent behaviour: subordinate walking towards the banana. Target behaviour: dominant walking towards the banana. After the subordinate walked towards the banana, the correlation coefficient of the dominant walking towards the banana is significantly more than expected from the within-trial shuffled control (peak at time= +12, $r=0.1388$, $n=666$; $-\log\text{-likelihood}=10.0735$, $p<0.05$). Furthermore, before the subordinate starts walking towards the banana, the dominant is significantly unlikely to walk towards the banana (peak at time= -3, -0.0716 , $n=893$; $-\log\text{-likelihood}=3.4877$, $p<0.05$).

When the subordinate walked towards the cucumber, the dominant also walked towards the cucumber significantly more than expected from the within-trial shuffled control (Figure 7.3); the dominant did not walk towards the cucumber before the subordinate walked, but the dominant did several seconds later.

Cross Correlation, Pair 1 *Unequal Rewards*: When the Subordinate Walks Towards the Cucumber, Does the Dominant Walk Towards the Cucumber?

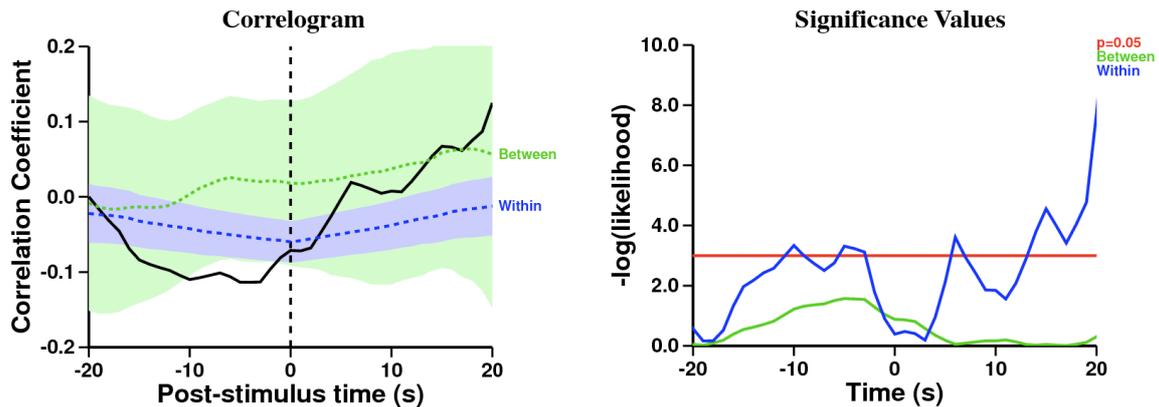


FIGURE 7.3: Referent behaviour: subordinate walking towards the cucumber. Target behaviour: dominant walking towards the cucumber. After the subordinate walked towards the cucumber, the correlation coefficient of the dominant walking towards the cucumber is significantly more than expected from the within-trial shuffled control (peak at time= +20, $r=0.1249$, $n=525$; $-\log\text{-likelihood}=7.7333$, $p<0.05$). Furthermore, before the subordinate started walking towards the cucumber, the dominant was significantly unlikely to walk towards the cucumber (peak at time= -10, $r=-0.1100$, $n=783$; $-\log\text{-likelihood}=3.3374$, $p<0.05$).

The dominant thus appeared to walk towards whichever bait that the subordinate moved towards.

E. Analysis of Gazing Towards the Two Baits

When the subordinate gazed towards the banana, the dominant was significantly likely to gaze towards the banana (see Figure 7.4). Both before and after the subordinate gazed towards the cucumber, the dominant was significantly likely to gaze towards the cucumber (see Figure 7.5).

Cross Correlation, Pair 1 *Unequal Rewards*: When the Subordinate Gazes Towards the Banana, Does the Dominant Gaze Towards the Banana?

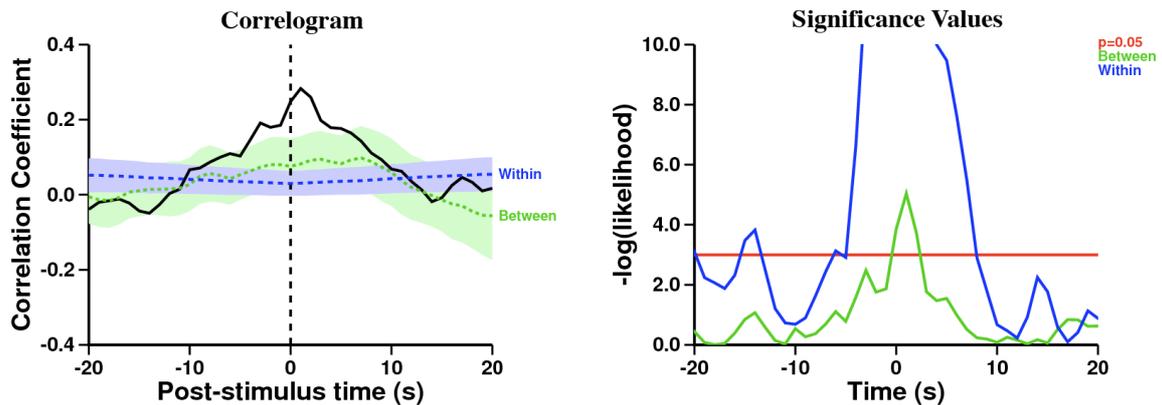


FIGURE 7.4: Referent behaviour: subordinate gazing towards the banana. Target behaviour: dominant gazing towards the banana. After the subordinate gazed towards the banana, the correlation coefficient of the dominant gazing towards the banana is significantly more than expected from the within-trial shuffled control (peak at time= +1, $r = 0.2829$, $n = 882$; $-\log\text{-likelihood} = 29.8341$, $p < 0.05$).

Cross Correlation, Pair 1 *Unequal Rewards*: When the Subordinate Gazes Towards the Cucumber, Does the Dominant Gaze Towards the Cucumber?

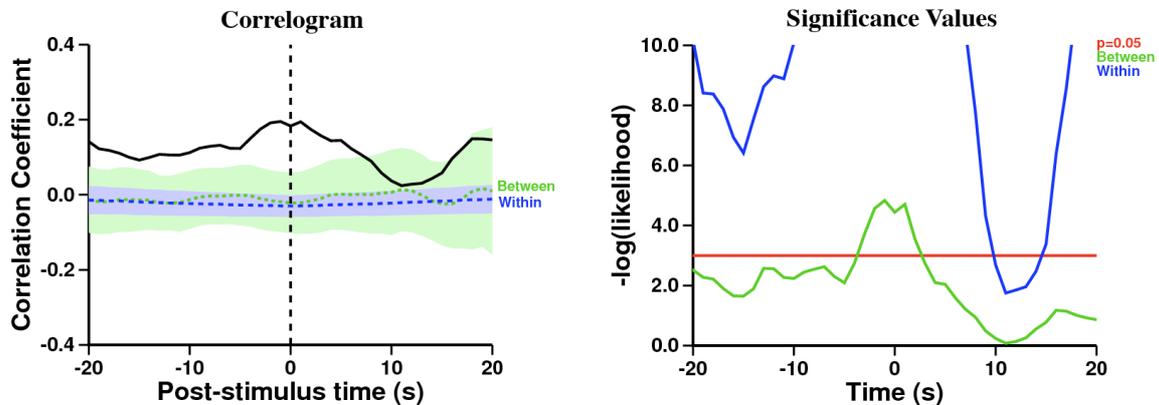


FIGURE 7.5: Referent behaviour: subordinate gazing towards the cucumber. Target behaviour: dominant gazing towards the cucumber. After the subordinate gazed towards the cucumber, the correlation coefficient of the dominant gazing towards the cucumber is significantly more than expected from the within-trial shuffled control (peak at time= +1, $r=0.1943$, $n=882$; $-\log\text{-likelihood}=31.0918$, $p<0.05$).

Both chimpanzees appeared to gaze towards both baits at approximately the same time; it is unclear whether either subject depended on gaze cues from the other.

F. Analysis of *Monitoring* and *Recruitment* Glances

This section addresses four questions: (i) Does the subordinate alternate her gaze between the dominant and the bait (banana/cucumber) while walking towards that bait (i.e., uses *monitoring* glances)? (ii) Does the dominant walk towards the bait when the subordinate alternates her gaze in this manner? (iii) Does the subordinate pause walking when she alternates her gaze in this manner (i.e., uses *recruitment* glances)? and (iv) Does the dominant walk towards the bait when the subordinate stops in this manner? All further analyses will have the subordinate's behaviour as the referent at time= 0 (cross correlations with the dominant as the referent are included in the appendix to Chapter 7).

1. Does the Subordinate Use *Monitoring* Glances?

Before the subordinate walked towards the banana, she looked at the dominant and then gazed towards the banana (Figure 7.6). The subordinate did not use *monitoring* glances after she started walking towards the banana.

Cross Correlation, Pair 1 *Unequal Rewards*: When the Subordinate Walks Towards the Banana, Does the Subordinate Look at the Dominant and then Gaze Towards the Banana?

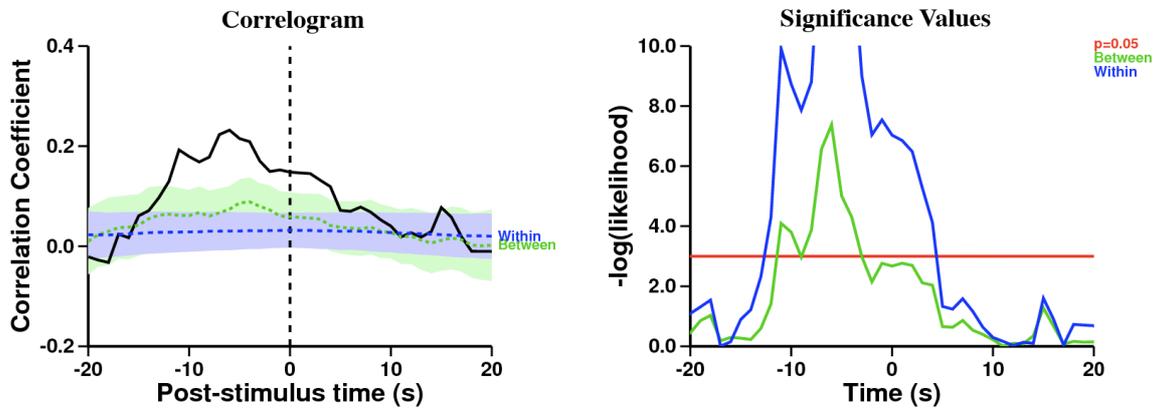


FIGURE 7.6: Referent behaviour: subordinate walking towards the banana. Target behaviour: subordinate looks at the dominant and then gazes towards the banana for two seconds. Before the subordinate started walking towards the banana, she looked at the dominant and then gazed towards the banana significantly more than expected from the within-trial shuffled control (peak at time= -6, $r = 0.2319$, $n = 783$; $-\log(\text{likelihood}) = 15.5885$, $p < 0.05$).

Similarly, the subordinate looked at the dominant and then gazed towards the cucumber before she walked towards the cucumber, but after she started walking she was significantly unlikely to use *monitoring* glances (Figure 7.7).

Cross Correlation, Pair 1 *Unequal Rewards*: When the Subordinate Walks Towards the Cucumber, Does the Subordinate Look at the Dominant and then Gaze Towards the Cucumber?

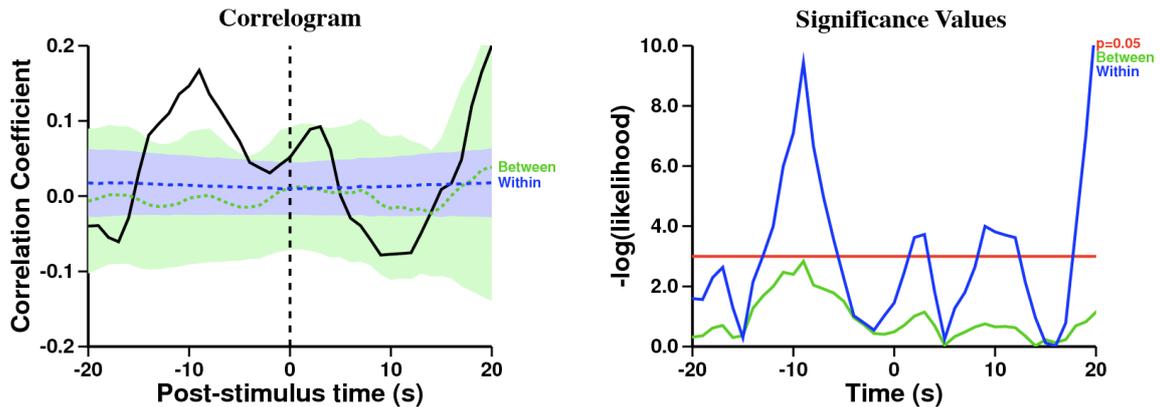


FIGURE 7.7: Referent behaviour: subordinate walking towards the cucumber. Target behaviour: subordinate looks at the dominant and then gazes towards the cucumber for two seconds. Before the subordinate started walking towards the cucumber, she looked at the dominant and then gazed towards the cucumber significantly more than expected from the within-trial shuffled control (peak at time= -9, $r = 0.1673$, $n = 721$; $-\log\text{-likelihood} = 9.4407$, $p < 0.05$). After the subordinate started walking towards the cucumber, she alternated gaze significantly more than expected (peak at time= +3, $r = 0.0924$, $n = 893$; $-\log\text{-likelihood} = 3.7263$, $p < 0.05$), and then significantly less than expected from the within-trial shuffled control (peak at time= +9, $r = -0.0783$, $n = 764$; $-\log\text{-likelihood} = 3.9983$, $p < 0.05$).

The subordinate used *monitoring* glances towards either hidden food item only before she started walking towards one. After the subordinate began walking towards a bait, she did not alternate her gaze between the dominant and the bait.

2. Does the Dominant Walk Towards the Bait When the Subordinate Uses *Monitoring Glances*?

The dominant was likely to be walking towards the banana before the subordinate used *monitoring* glances towards it, but after the subordinate looked at the dominant and then gazed towards the banana, the dominant only walked towards the banana for a brief time before she was less likely to do so (Figure 7.8).

Cross Correlation, Pair 1 *Unequal Rewards*: When the Subordinate Uses *Monitoring Glances* Towards the Banana, Does the Dominant Walk Towards the Banana?

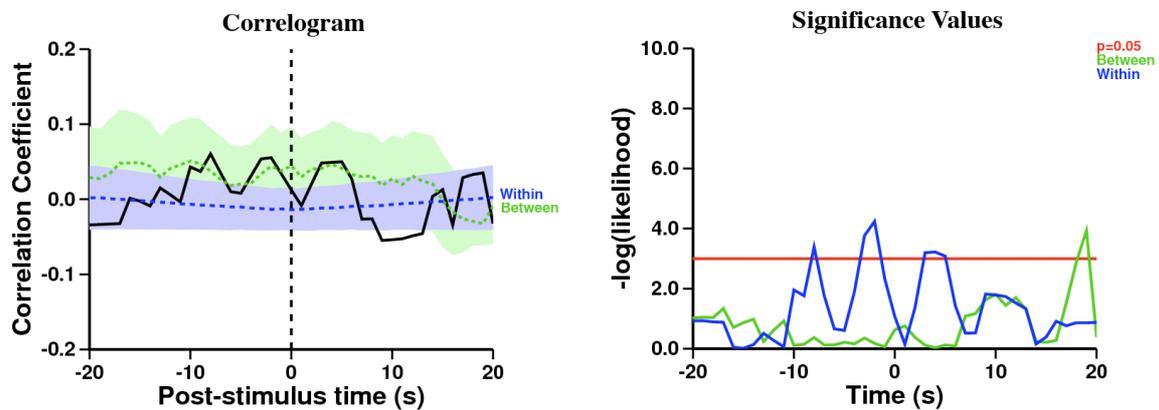


FIGURE 7.8: Referent behaviour: subordinate looks at the dominant and then gazes towards the banana for two seconds. Target behaviour: dominant walking towards the banana. Both before and after the subordinate uses *monitoring* glances, the dominant walked towards the banana significantly more than expected from the within-trial shuffled control (peak at time = -8, $r = 0.0604$, $n = 816$; $-\log\text{-likelihood} = 3.3895$, $p < 0.05$. Time = -2, $r = 0.0554$, $n = 852$; $-\log\text{-likelihood} = 4.2400$, $p < 0.05$. Time = +4, $r = 0.0491$, $n = 780$; $-\log\text{-likelihood} = 3.2199$, $p < 0.05$).

The dominant walked towards the cucumber before, during, and after the subordinate used *monitoring* glances towards it (Figure 7.9).

Cross Correlation, Pair 1 *Unequal Rewards*: When the Subordinate Uses *Monitoring* Glances Towards the Cucumber, Does the Dominant Walk Towards the Cucumber?

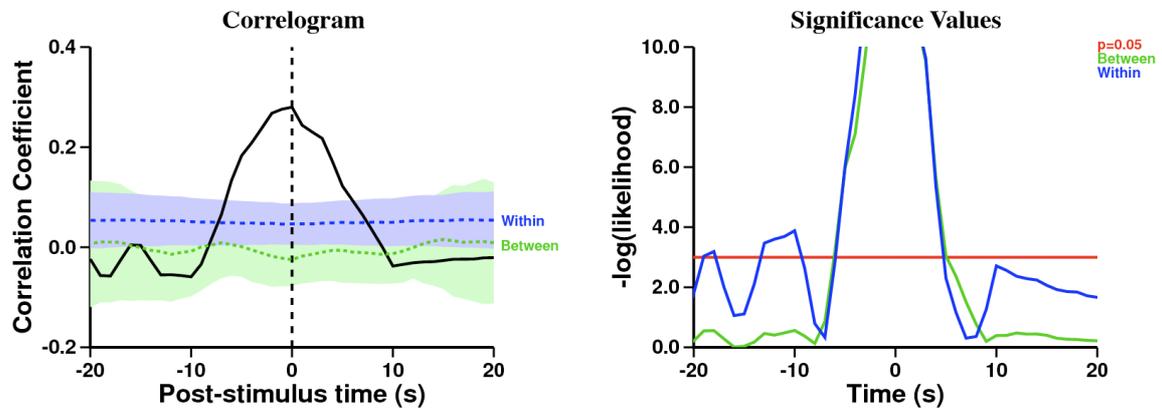


FIGURE 7.9: Referent behaviour: subordinate looks at the dominant and then gazes towards the cucumber for two seconds. Target behaviour: dominant walking towards the cucumber. Before, during, and after the subordinate uses *monitoring* glances, the dominant walked towards the cucumber significantly more than expected from the within-trial shuffled control (peak at time= 0, $r = 0.2798$, $n = 856$; $-\log\text{-likelihood} = 17.9298$, $p < 0.05$).

The subordinate's *monitoring* cue towards the cucumber did not seem to have an influence on the dominant—she was already walking towards the cucumber when the subordinate alternated her gaze. But when the subordinate used *monitoring* glances towards the banana, the dominant was less likely to continue walking towards the banana. The *monitoring* glance itself was not essential for the dominant to find the hidden baits.

3. Does the Subordinate Use *Recruitment* Glances?

Many seconds after the subordinate looked at the dominant and then gazed towards the banana, she stopped walking for five seconds (Figure 7.10).

Cross Correlation, Pair 1 *Unequal Rewards*: When the Subordinate Uses *Monitoring* Glances Towards the Banana, Does the Subordinate Stop Walking?

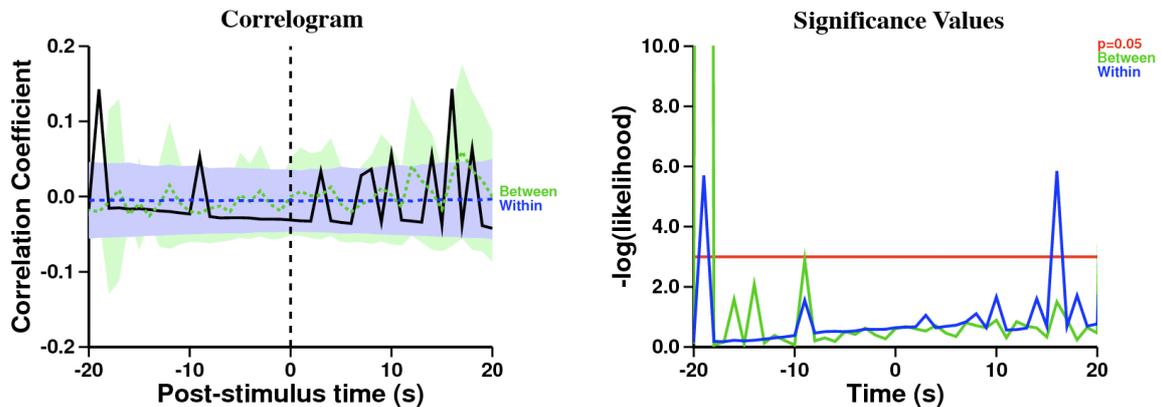


FIGURE 7.10: Referent behaviour: subordinate looks at the dominant and then gazes towards the banana for two seconds. Target behaviour: subordinate stops walking for five seconds. Many seconds after the subordinate uses *monitoring* glances, the subordinate stops walking (peak at time= +16, $r = 0.1432$, $n = 303$; $-\log\text{-likelihood} = 5.8473$, $p < 0.05$). Long before the subordinate uses *monitoring* glances, she stops, though this may be an artefact of the experimental setup (peak at time= -19, $r = 0.1427$, $n = 346$; $-\log\text{-likelihood} = 5.7040$, $p < 0.05$).

Several seconds after the subordinate looked at the dominant and then gazed towards the cucumber, she stopped walking for five seconds (Figure 7.11).

Cross Correlation, Pair 1 *Unequal Rewards*: When the Subordinate Uses *Monitoring* Glances Towards the Cucumber, Does the Subordinate Stop Walking?

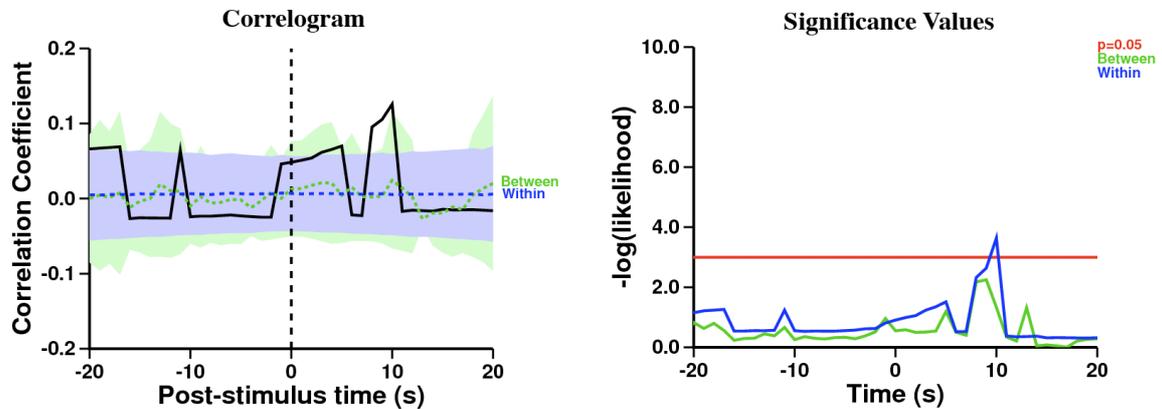


FIGURE 7.11: Referent behaviour: subordinate looks at the dominant and then gazes towards the cucumber for two seconds. Target behaviour: subordinate stops walking for five seconds. Several seconds after the subordinate uses *monitoring* glances, the subordinate stops walking (peak at time= +10, $r = 0.1258$, $n = 391$; $-\log\text{-likelihood} = 3.6366$, $p < 0.05$).

The subordinate was significantly likely to pause in her walking after alternating gaze between the dominant and either bait; however, her pause did not immediately follow her gaze alternation and is thus not a *recruitment* glance as I have defined it for this analysis.

4. Does the Dominant Walk Towards the Bait When the Subordinate Uses *Recruitment* Glances?

Though the previous correlograms (Figures 7.10 and 7.11) showed that the subordinate did not immediately pause after alternating her gaze, there were a few instances (five times total) in which she did pause immediately, thus showing *recruitment* glances. On those occasions, the pattern in the correlogram in Figure 7.12 indicates that the dominant walked towards the banana after the subordinate used the *recruitment* glance, though this relationship was not significantly different from the within-trial shuffled control, due to low sample size.

Cross Correlation, Pair 1 *Unequal Rewards*: When the Subordinate Uses *Recruitment* Glances Towards the Banana, Does the Dominant Walk Towards the Banana?

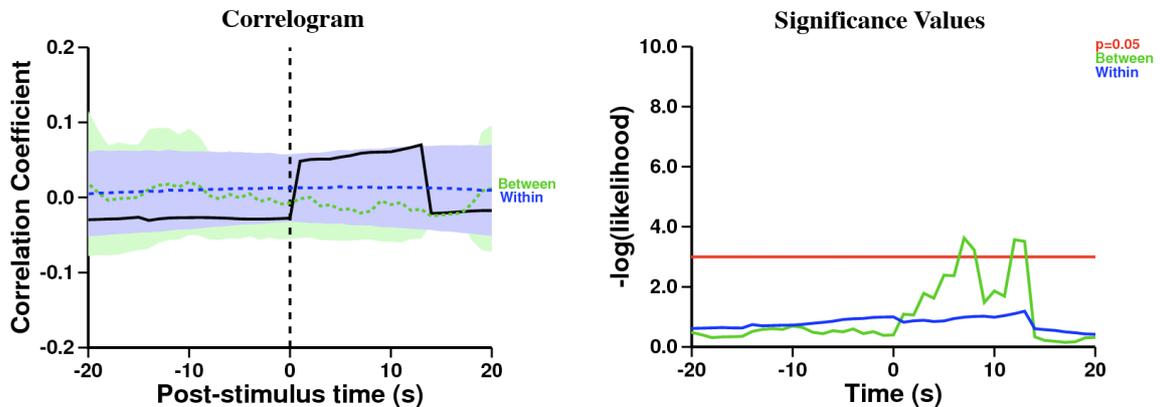


FIGURE 7.12: Referent behaviour: subordinate gazes towards the banana for two seconds, while stopping locomotion for five seconds. Target behaviour: dominant walking towards the banana. The pattern in the correlogram indicates that the dominant walked towards the banana after the subordinate used *recruitment* glances, but there is no significant relationship between the two variables (peak at time= +13, $r = 0.0701$, $n = 417$; $-\log\text{-likelihood} = 1.1873$, *ns*).

Similarly, when the subordinate did *recruit* towards the cucumber, the dominant walked towards the cucumber, and this relationship trended towards being more than expected from the within-trial shuffled control, due to low sample size (Figure 7.13).

Cross Correlation, Pair 1 *Unequal Rewards*: When the Subordinate Uses *Recruitment* Glances Towards the Cucumber, Does the Dominant Walk Towards the Cucumber?

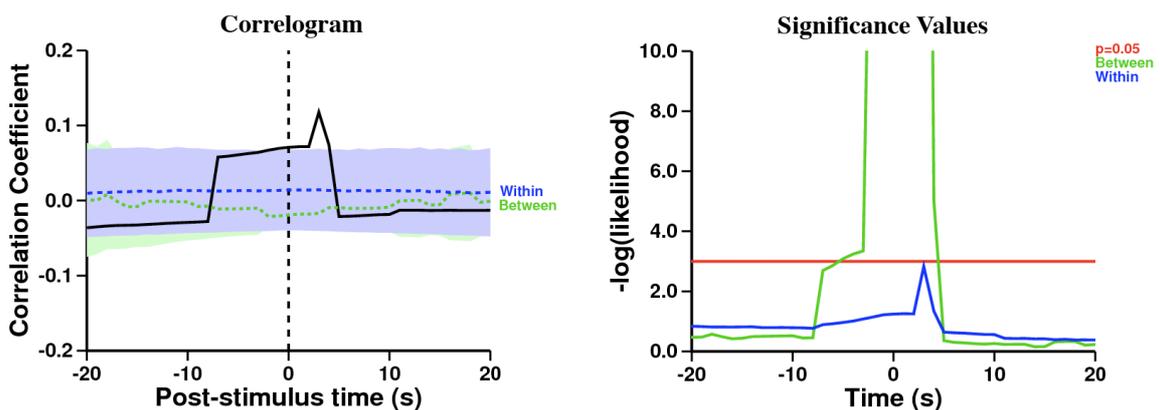


FIGURE 7.13: Referent behaviour: subordinate gazes towards the cucumber for two seconds, while stopping locomotion for five seconds. Target behaviour: dominant walking towards the cucumber. After the subordinate used *recruitment* glances, the dominant walked towards the cucumber, and this relationship trends towards being more than expected from the within-trial shuffled control (peak at time= +3, $r = 0.1177$, $n = 558$; $-\log\text{-likelihood} = 2.8262$, *ns*).

It appears that on the few occasions that the subordinate did use *recruitment* glances, the dominant did walk towards the bait that the subordinate *recruited* towards, though the relationships are not significant.

IV. Discussion: Pair 1

The subordinate used *monitoring* glances before walking towards either bait, and paused in her movement ten seconds (cucumber) and sixteen seconds (banana) after her initial *monitoring* glance. Since her movement pause was not immediate (as I have defined it for this analysis), it cannot be considered a *recruitment* glance. The length of time between the *monitoring* glance and movement pause suggests that it is possible that the subordinate's pause occurred while she searched for the bait and that she was not attempting to *recruit* the dominant to approach. When the subordinate did use *recruitment* glances I have defined them, the dominant appeared to walk towards the bait that the subordinate *recruited* towards. Perhaps the subordinate's *monitoring* glance before walking towards the banana was used to check on whether the dominant was looking or moving towards the banana, and if not, the subordinate then started walking. Her *monitoring* glances did not seem to encourage the dominant to walk towards the banana for more than a few seconds. The subordinate used *monitoring* glances before walking towards the cucumber, and the dominant walked towards the cucumber before and after the subordinate used *monitoring* glances, suggesting that the subordinate *monitored* to make sure that the dominant continued following.

Subordinate Missy did not use proper *recruitment* glances often—five times total—and dominant Rita reacted by walking towards the bait on two of those occasions (and picked up the banana that Missy had glanced to on one trial). This can help explain why the correlograms addressing whether the dominant walked towards the bait after the subordinate *recruited* are not significantly different from the within-trial shuffled control: small sample size. It is difficult to draw any conclusions from so few instances of the behaviour; the dominant did not seem to follow or exploit the subordinate much in this experiment, so perhaps the subordinate did not need to distract the dominant away from the banana and towards the cucumber.

V. Results: Pair 2

A. Results of Preference Test

Each subject was individually tested for her preference between banana and cucumber. Subordinate Reinette chose banana in 10 out of 10 choices, and dominant Georgia chose banana 9 out of 10 times.

B. Who Found the Rewards?

The subordinate, Reinette, was informed of the location of a hidden banana and a hidden cucumber on the twenty *Unequal Reward* trials. Reinette obtained slightly fewer than half of the rewards: 8 bananas and 9 cucumbers (42.5% of total rewards); dominant competitor Georgia picked up 11 bananas and 9 cucumbers (50% of total) (Figure 7.14). One banana (trial 10) and two cucumbers (trials 4 and 7) were not picked up. These percentages are different from the one reward *Competition*, indicating that Georgia increased her exploitation of Reinette's foraging success.

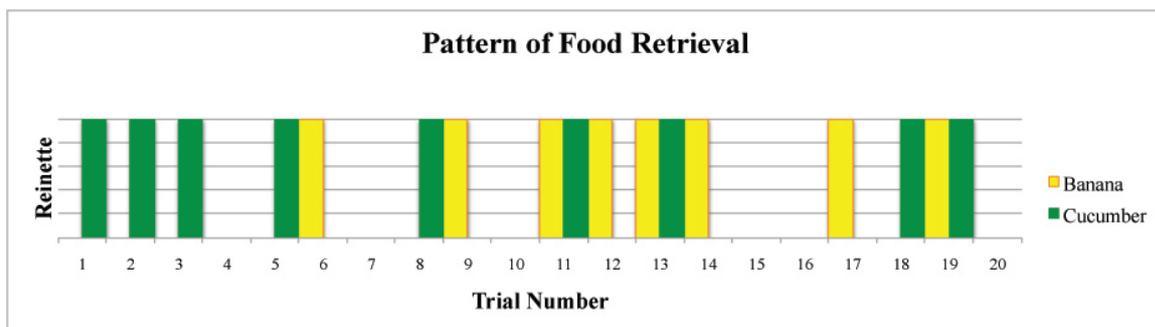


FIGURE 7.14: Pattern of the Subordinate's Food Retrieval, Pair 2

Georgia was first to pick up a reward on sixteen trials. The average trial length was 95.4 seconds. The average time to find the banana was 70.4 seconds, and to find the cucumber was 73.0 seconds. The subordinate approached the banana before the cucumber on ten trials.

Knowledgeable subordinate Reinette did not retrieve the bait that she first approached on twelve trials, and she made no approach at all on three trials. The bait that she approached first was picked up second on five trials, of which dominant Georgia picked up two food items. On the three trials that Reinette did not approach either bait, Georgia was able to search and find one of the baits, and in all cases, the bait that Georgia found was hidden in Quadrant 3, closest to the chimpanzees' starting position in the 'Cognition Room.'

C. Descriptive Account of *Unequal Rewards*

During the course of the *Unequal Rewards* experiment, the dominant paid very close attention to the subordinate's direction of gaze and movement, and was very quick to change her own direction and run ahead of the subordinate to exploit her. On the first trial, the subordinate found the cucumber under the red ring in Q4, and as she changed direction to walk towards the banana, the dominant walked ahead of her and found it in the Q1 culvert before the subordinate arrived at the location. On the second trial the dominant found the banana by her own search in the hanging tire, then *converged* on the subordinate's destination to the other end of the enclosure in Quadrant 2, though the subordinate picked up the cucumber before the dominant could exploit her. On the third trial, the dominant ran ahead of the subordinate: and on two occasions, as soon as the subordinate changed her direction of movement, so did the dominant. The subordinate then walked around the perimeter of the enclosure, giving no indication of searching for hidden food. The dominant found the banana in the Q1 tire by searching randomly, and after she uncovered it, the subordinate changed direction again and walked to Quadrant 4. The dominant followed her and started searching in that area, as the subordinate again walked along the perimeter towards Quadrant 2. The subordinate glanced back at the dominant before picking up the cucumber in Q2. On the next trial, the dominant found the banana under the kegs in Q3, and after the subordinate inspected that (empty) hiding place, she returned inside and neither subject found the cucumber. On trial five, the subordinate ran towards where the banana was hidden, and the dominant ran in her *footsteps*. The subordinate threatened the dominant, but then ran away and threw a tantrum, screaming loudly in protest as the dominant uncovered the banana. The subordinate sat against the 'Cognition Room' wall as the dominant *approached* and threatened her. The subordinate walked along the enclosure perimeter then returned to where the banana had been, as the dominant *approached* and *converged* to arrive in the same location. The subordinate then turned away and picked up the cucumber in the Q1 hammock.

On trial six, the dominant took the cucumber; the subordinate looked back at the dominant several times while walking to where the banana was hidden, and waited until the dominant's back was turned before retrieving the reward. On trial seven, the dominant found the banana and neither subject picked up the cucumber. After the dominant found the banana on the eighth trial, she sat on top of the white barrel in Quadrant 1 as she ate. The subordinate

attempted to search underneath the barrel for the cucumber, but then walked to where the dominant had found the banana in Q2. When the dominant left her position on the white barrel, the subordinate returned, glanced back at the dominant, and then finally uncovered the cucumber, 1:47 minutes after the dominant had first sat there. The subordinate also had to wait for the dominant on the ninth trial: the dominant followed the subordinate's every move until they were both at the location of the banana under the red ring in Q4. The dominant searched under it but did not find the reward, and the subordinate sat next to it, looking in the opposite direction, for 2:05 minutes until the dominant left the area and the subordinate's patience paid off and she picked up the banana. The dominant found the banana on the next trial, and neither chimpanzee picked up the cucumber.

On the eleventh trial, the chimpanzees walked in parallel towards the tire in Quadrant 1; the dominant searched there but did not find anything. The subordinate glanced at the dominant as she walked away, and found the cucumber in the tire. The dominant returned to search again, as the subordinate searched in Quadrant 2 for the banana. On trial twelve, as the subordinate searched in the Q4 culvert, the dominant took the cucumber from her. Later, the subordinate was careful to glance at the dominant before searching for the banana under the kegs in Q3. Though the dominant used all three following tactics on the next trial, the subordinate retrieved both baits. On trial fourteen, the dominant again picked up the cucumber, and the subordinate got the banana. On trial fifteen, the dominant found both rewards.

The dominant continued to exploit the subordinate on trial sixteen: she *approached* the subordinate and then followed in her *footsteps*, walked ahead and found the banana under the barrel in Q1, continuing to follow her and find the cucumber under the box in Q2. The dominant found the cucumber and the subordinate found the banana on the next trial. After finding the banana on trial eighteen, the dominant climbed onto the structure to eat, allowing the subordinate to find the cucumber without exploitation. On trial nineteen, the dominant followed the subordinate's movement closely but as soon as the dominant was a few steps away the subordinate picked up the banana from the tire in Q1. Then the subordinate walked along the perimeter of the enclosure to where the cucumber was hidden in Q2. On the last trial the dominant followed in the *footsteps* of the subordinate and found the cucumber, then again ran after the subordinate to take the banana.

The dominant closely followed the subordinate's gaze and movement in order to exploit her foraging success, and though she did find some rewards by searching familiar locations, it seemed that on many trials the dominant was able to use some visual or movement cue from the subordinate to find the food (Correlograms with *approach*, *footsteps*, *convergence*, and *static gaze* are included in the appendix to Chapter 7).

D. Analysis of Walking Towards the Two Baits

Here I use cross correlations to address the subjects' movement towards the two hidden baits, banana and cucumber. Only the subordinate had seen where the two food items were hidden on each trial. Previous analyses for this pair showed that there was no relationship between the subordinate walking towards the bait and the dominant walking towards the bait (See Chapter 5: Movement Following). However, it appeared that the dominant followed the subordinate very closely in the *Unequal Reward* condition and so I again asked, "When the subordinate walks towards the banana, does the dominant walk towards the banana?" and also, "When the subordinate walks towards the cucumber, does the dominant walk towards the cucumber?"

There was a very strong relationship between the two chimpanzees walking towards the banana in the *Unequal Reward* experiment: after the subordinate started walking towards the banana, the dominant walked towards the banana (See Figure 7.15). Data are compared to the within-trial shuffled control; this particular control is used because the bait is in a different location on each trial.

Cross Correlation, Pair 2 *Unequal Rewards*: When the Subordinate Walks Towards the Banana, Does the Dominant Walk Towards the Banana?

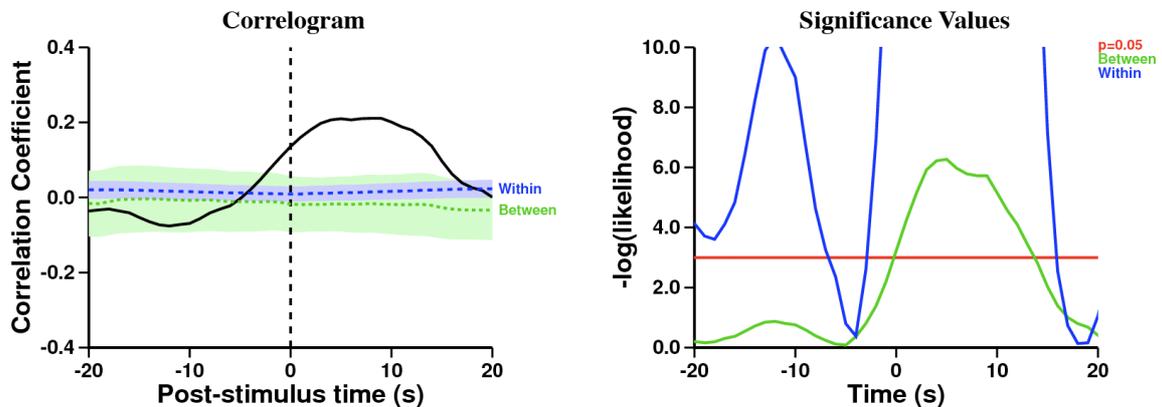


FIGURE 7.15: Referent behaviour: subordinate walking towards the banana. Target behaviour: dominant walking towards the banana. After the subordinate walked towards the banana, the correlation coefficient of the dominant walking towards the banana is significantly more than expected from the within-trial shuffled control (peak at time= +4, $r=0.2066$, $n=1763$; $-\log\text{-likelihood}=45.7881$, $p<0.05$). Furthermore, before the subordinate started walking towards the banana, the dominant was significantly unlikely to walk towards the banana (peak at time= -12, $r=-0.0761$, $n=1665$; $-\log\text{-likelihood}=10.4127$, $p<0.05$).

Additionally, there was a strong relationship of the dominant walking towards the cucumber after the subordinate started walking towards it (see Figure 7.16).

Cross Correlation, Pair 2 *Unequal Rewards*: When the Subordinate Walks Towards the Cucumber, Does the Dominant Walk Towards the Cucumber?

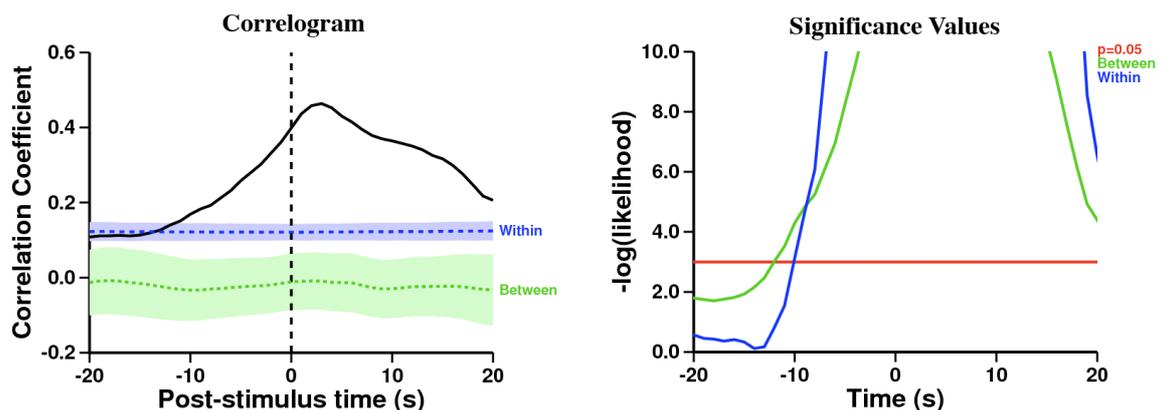


FIGURE 7.16: Referent behaviour: subordinate walking towards the cucumber. Target behaviour: dominant walking towards the cucumber. After the subordinate walked towards the cucumber, the correlation coefficient of the dominant walking towards the cucumber is significantly more than expected from the within-trial shuffled control (peak at time= +3, $r=0.4637$, $n=1782$; $-\log\text{-likelihood}=110.6573$, $p<0.05$).

When the subordinate walked towards either bait, the dominant walked towards the same bait as the subordinate.

E. Analysis of Gazing Towards the Two Baits

Both chimpanzees gazed towards the banana at approximately the same time (Figure 7.17) and that pattern remains the same for the cucumber (Figure 7.18).

Cross Correlation, Pair 2 *Unequal Rewards*: When the Subordinate Gazes Towards the Banana, Does the Dominant Gaze Towards the Banana?

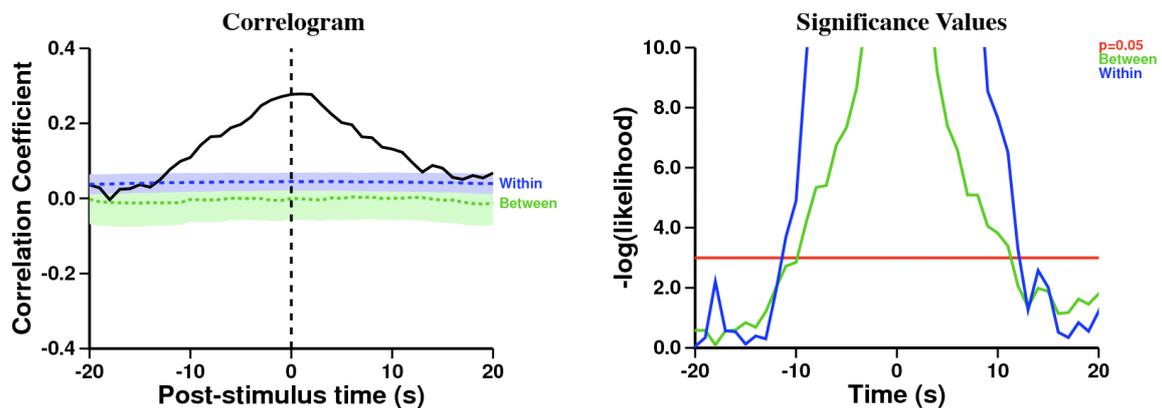


FIGURE 7.17: Referent behaviour: subordinate gazing towards the banana. Target behaviour: dominant gazing towards the banana. After the subordinate gazed towards the banana, the correlation coefficient of the dominant gazing towards the banana is significantly more than expected from the within-trial shuffled control (peak at time= 0, $r=0.2772$, $n=1857$; $-\log\text{-likelihood}=51.3762$, $p<0.05$).

Cross Correlation, Pair 2 *Unequal Rewards*: When the Subordinate Gazes Towards the Cucumber, Does the Dominant Gaze Towards the Cucumber?

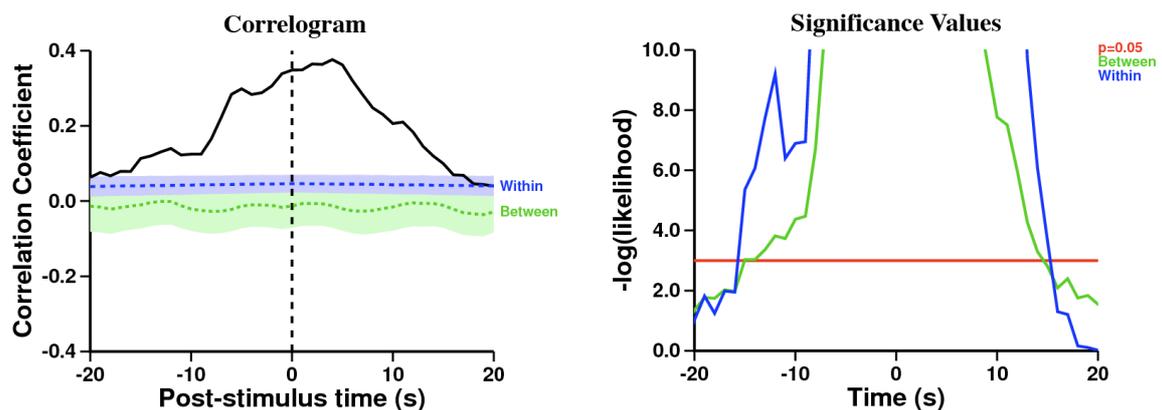


FIGURE 7.18: Referent behaviour: subordinate gazing towards the cucumber. Target behaviour: dominant gazing towards the cucumber. As shown above, after the subordinate gazes towards the cucumber, the correlation coefficient of the dominant gazing towards the cucumber is significantly higher than the within-trial shuffled control (peak at time= +4, $r=0.3762$, $n=1781$; $-\log\text{-likelihood}=92.4452$, $p<0.05$).

It remains unclear upon what cue each chimpanzee gazed towards either bait; they both appear to gaze at the same time towards the banana and the cucumber.

F. Analysis of *Monitoring* and *Recruitment* Glances

This analysis addresses four questions: (i) Does the subordinate alternate her gaze between the dominant and the bait (banana/cucumber) while walking towards that bait (i.e., uses *monitoring* glances)? (ii) Does the dominant walk towards the bait when the subordinate alternates her gaze in this manner? (iii) Does the subordinate pause walking when she alternates her gaze in this manner (i.e., uses *recruitment* glances? and (iv) Does the dominant walk towards the bait when the subordinate stops in this manner? All further analyses will have the subordinate's behaviour as the referent at time= 0 (cross correlations with the dominant as the referent are included in the appendix to Chapter 7).

1. Does the Subordinate Use *Monitoring* Glances?

Before the subordinate walked towards the banana, she looked at the dominant and then gazed towards the banana (Figure 7.19). The subordinate only seemed to use *monitoring* glances before walking towards the banana; after the subordinate began walking towards the banana, she no longer alternated gaze between her opponent and the bait.

Cross Correlation, Pair 2 *Unequal Rewards*: When the Subordinate Walks Towards the Banana, Does the Subordinate Look at the Dominant and then Gaze Towards the Banana ?

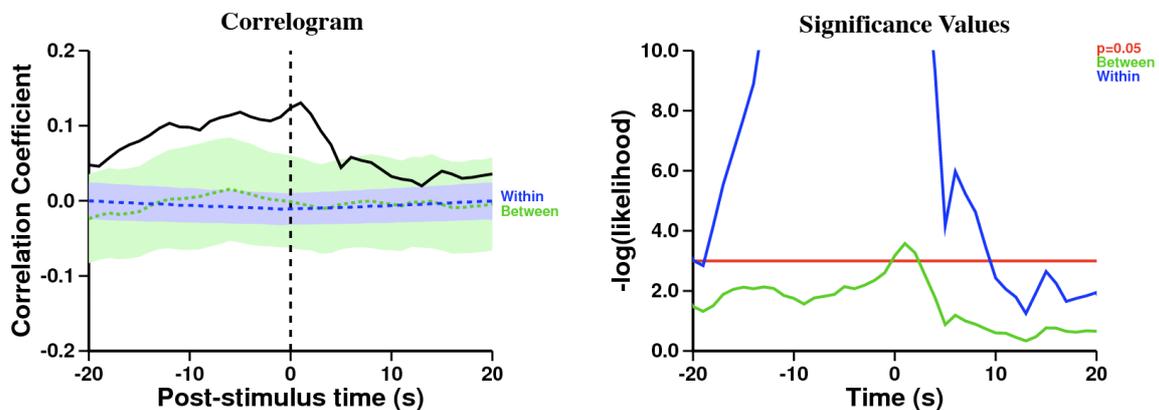


FIGURE 7.19: Referent behaviour: subordinate walking towards the banana. Target behaviour: subordinate looks at the dominant and then gazes towards the banana for two seconds. Before, during, and after the subordinate walked towards the banana, she looked at the dominant and then gazed towards the banana significantly more than expected from the within-trial shuffled control (peak at time= +1, $r = 0.1305$, $n = 1815$; $-\log\text{-likelihood} = 23.9195$, $p < 0.05$).

Before, during, and after the subordinate walked towards the cucumber, she alternated gaze between the dominant and the cucumber (Figure 7.20). The subordinate used *monitoring* gaze throughout the time she walked towards the cucumber.

Cross Correlation, Pair 2 *Unequal Rewards*: When the Subordinate Walks Towards the Cucumber, Does the Subordinate Look at the Dominant and then Gaze Towards the Cucumber ?

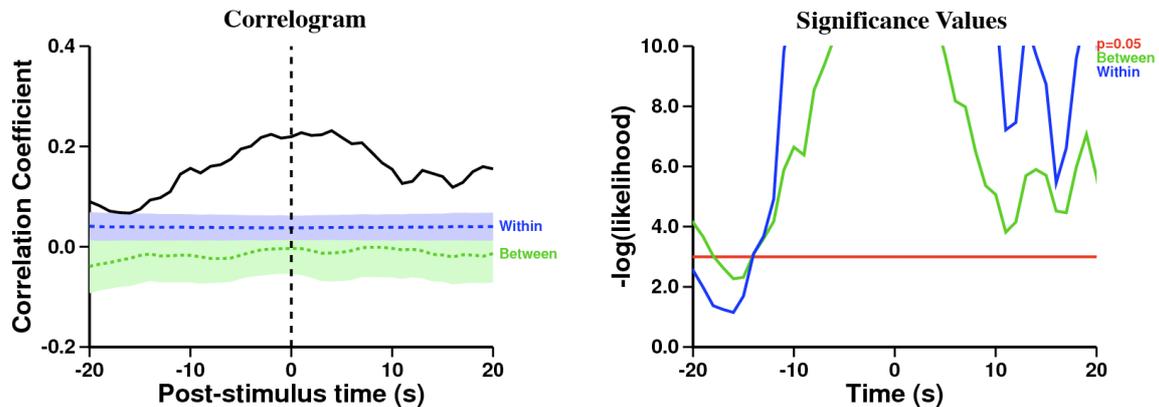


FIGURE 7.20: Referent behaviour: subordinate walking towards the cucumber. Target behaviour: subordinate looks at the dominant and then gazes towards the cucumber for two seconds. Before, during, and after the subordinate walked towards the cucumber, she looked at the dominant and then gazed towards the cucumber significantly more than expected from the within-trial shuffled control (peak at time= +4, $r = 0.2314$, $n = 1774$; $-\log\text{-likelihood} = 32.0526$, $p < 0.05$).

The subordinate used *monitoring* glances before approaching either bait, but only continued *monitoring* the dominant while walking towards the cucumber, but not towards the banana.

2. Does the Dominant Walk Towards the Bait When the Subordinate Uses *Monitoring Glances*?

Though the subordinate only *monitored* the dominant before walking towards the banana, the dominant walked towards the banana both before and after the subordinate *monitored*, indicating that the dominant may have been relying more on the subordinate's movement towards the banana (Figure 7.21).

Cross Correlation, Pair 2 *Unequal Rewards*: When the Subordinate uses *Monitoring Glances* Towards the Banana, Does the Dominant Walk Towards the Banana?

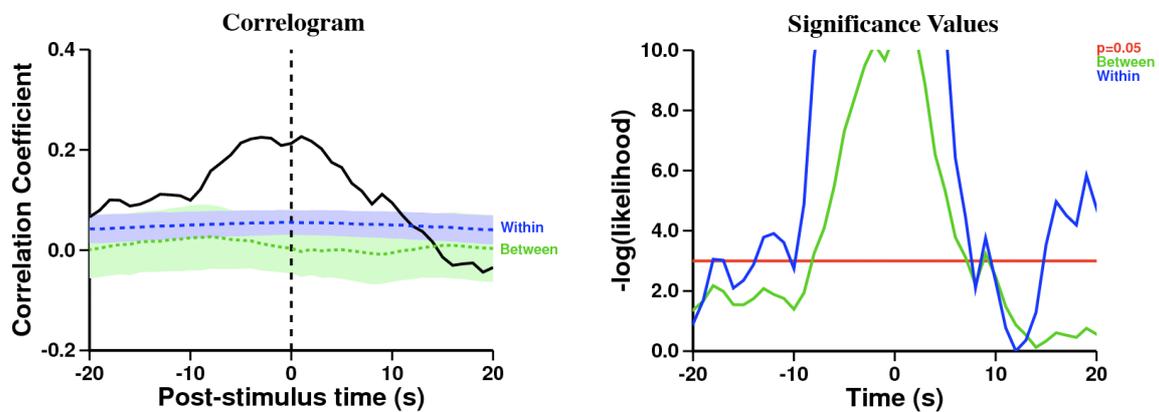


FIGURE 7.21: Referent behaviour: subordinate looks at the dominant and then gazes towards the banana for two seconds. Target behaviour: dominant walking towards the banana. Before, during, and after the subordinate used *monitoring* glances, the dominant walked towards the banana significantly more than expected from the within-trial shuffled control (peak at time= +1, $r = 0.2264$, $n = 1781$; $-\log\text{-likelihood} = 26.4031$, $p < 0.05$).

The dominant walked towards the cucumber both before and after the subordinate used *monitoring* glances (Figure 7.22).

Cross Correlation, Pair 2 Unequal Rewards: When the Subordinate Uses *Monitoring* Glances Towards the Cucumber, Does the Dominant Walk Towards the Cucumber?

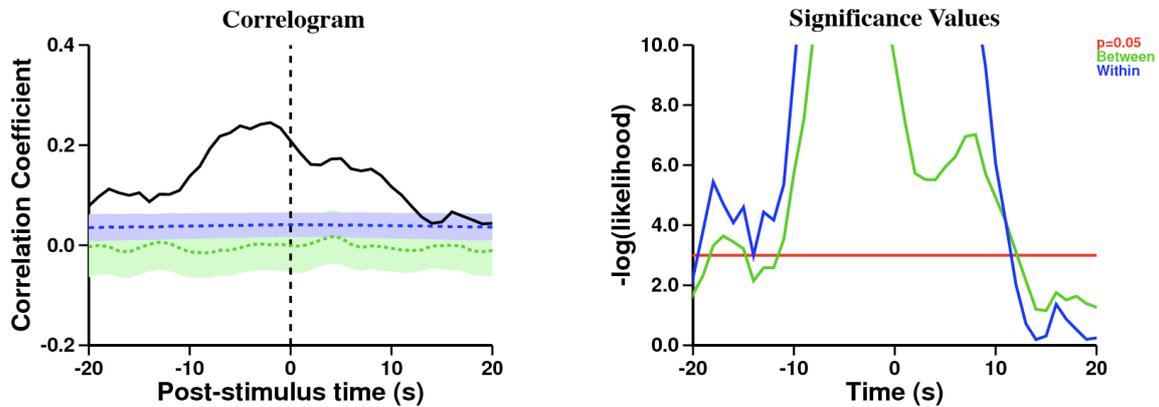


FIGURE 7.22: Referent behaviour: subordinate looks at the dominant and then gazes towards the cucumber for two seconds. Target behaviour: dominant walking towards the cucumber. Before, during, and after the subordinate used *monitoring* glances, the dominant walked towards the cucumber (peak at time = -2, $r = 0.2449$, $n = 1799$; $-\log\text{-likelihood} = 36.5533$, $p < 0.05$).

The dominant walked towards both baits before and after the subordinate *monitored* her, which suggests that the *monitoring* glance itself was not essential for the dominant to find the hidden baits.

3. Does the Subordinate Use *Recruitment* Glances?

When the subordinate used *monitoring* glances in conjunction with a five-second pause in her locomotion, her behaviour was classified as a *recruitment* glance. When the subordinate alternated gaze between the dominant and the banana, she did not pause her movement; the subordinate did not *recruit* towards the banana (Figure 7.23).

Cross Correlation, Pair 2 *Unequal Rewards*: When the Subordinate Uses *Monitoring* Glances Towards the Banana, Does the Subordinate Stop Walking?

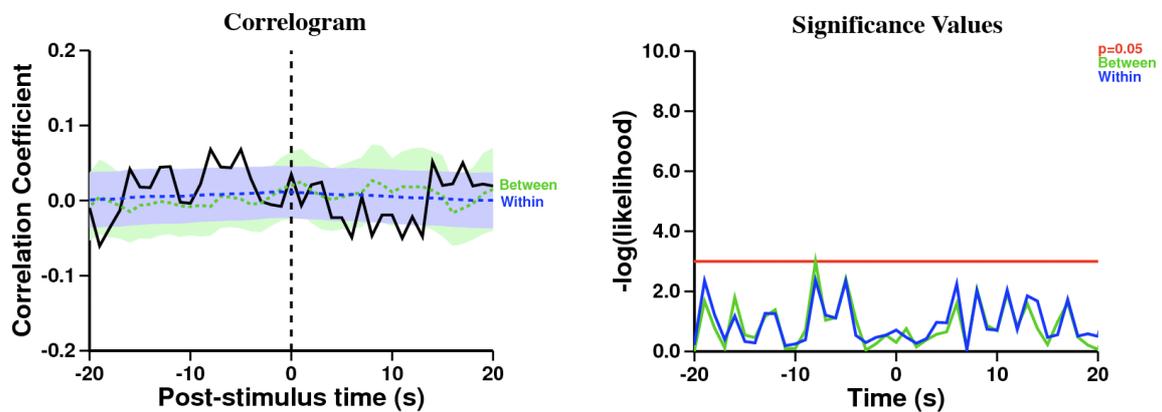


FIGURE 7.23: Referent behaviour: subordinate looks at the dominant and then gazes towards the banana for two seconds. Target behaviour: subordinate stops walking for five seconds. Before the subordinate used *monitoring* glances, she stopped walking, and this relationship trends towards being more than expected from the within-trial shuffled control (peak at time= -8, $r = 0.0681$, $n = 888$; $-\log\text{-likelihood} = 2.3693$, *ns*). After the subordinate used *monitoring* glances, she was unlikely to stop walking, and this relationship trends towards being less than expected from the within-trial shuffled control (peak at time= +6, $r = -0.0491$, $n = 815$; $-\log\text{-likelihood} = 2.2451$, *ns*).

When the subordinate alternated her gaze between the dominant and the cucumber, she did pause in her movement; the subordinate did *recruit* towards the cucumber (Figure 7.24). She paused nearly immediately after alternating her gaze, and therefore this should be considered a *recruitment* glance in the strict sense.

Cross Correlation, Pair 2 Unequal Rewards: When the Subordinate Uses *Monitoring* Glances Towards the Cucumber, Does the Subordinate Stop Walking?

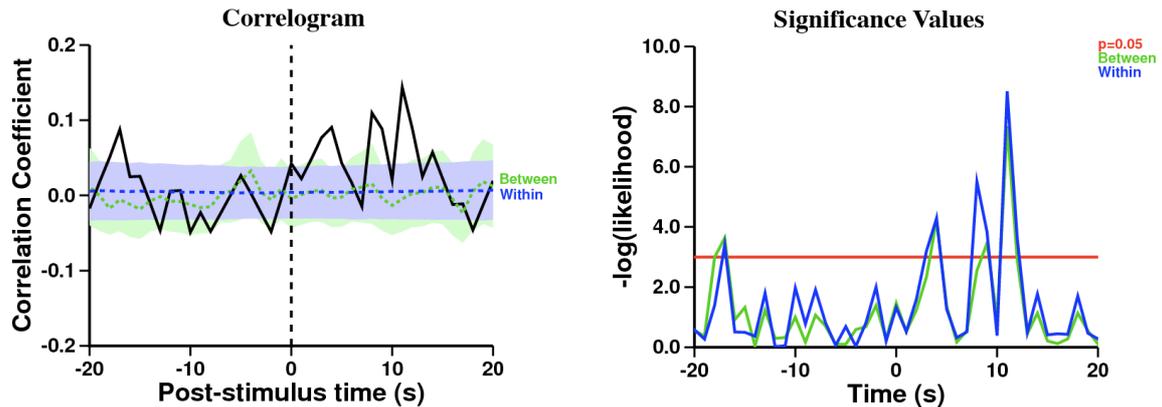


FIGURE 7.24: Referent behaviour: subordinate looks at the dominant and then gazes towards the cucumber for two seconds. Target behaviour: subordinate stops walking for five seconds. After the subordinate used *monitoring* glances, she stopped walking significantly more than expected from the within-trial shuffled control (beginning at time= +3, $r = 0.0769$, $n = 867$; $-\log\text{-likelihood} = 3.1979$, $p < 0.05$. Peak at time= +11, $r = 0.1437$, $n = 743$; $-\log\text{-likelihood} = 8.5099$, $p < 0.05$).

While using *monitoring* glances towards either bait, the subordinate was likely to stop walking only when she approached the cucumber, but not the banana. Thus, the subordinate only *recruited* the dominant towards the cucumber.

4. Does the Dominant Walk Towards the Bait When the Subordinate Uses Recruitment Glances?

Though the previous correlograms indicated that the subordinate did not recruit towards the banana (Figure 7.23), she did on occasion pause after alternating gaze between the dominant and the banana. After the subordinate did use *recruitment* glances towards the banana, the dominant walked towards the banana (Figure 7.25).

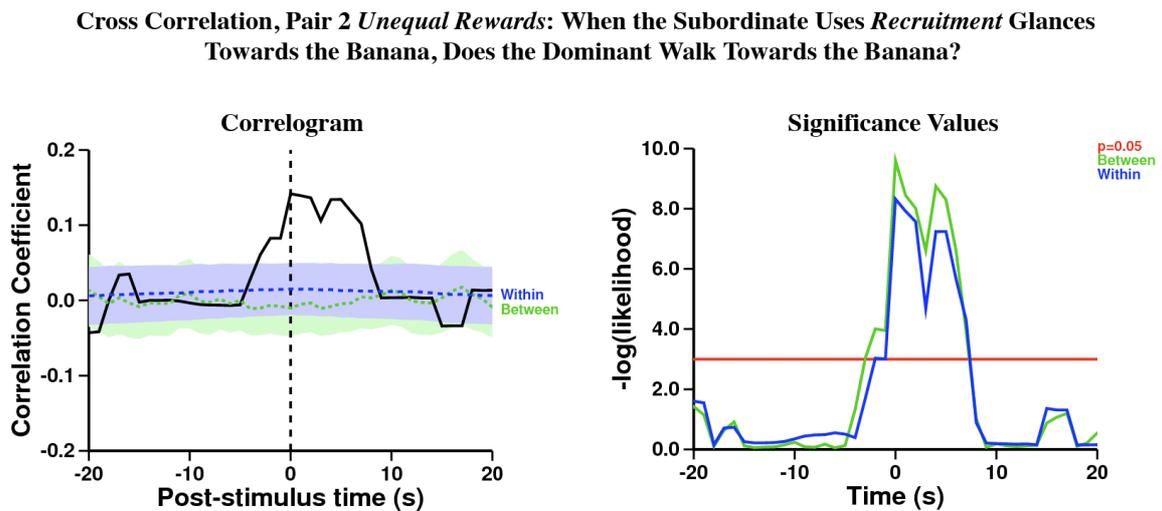


FIGURE 7.25: Referent behaviour: subordinate gazes towards the banana for two seconds, while stopping locomotion for five seconds. Target behaviour: dominant walking towards the banana. After the subordinate used *recruitment* glances, the dominant walked towards the banana significantly more than expected from the within-trial shuffled control (peak at time=0, $r = 0.1417$, $n = 941$; $-\log(\text{likelihood}) = 8.3203$, $p < 0.05$).

The dominant was likely to be walking towards the cucumber before the subordinate used *recruitment* glances towards the cucumber (Figure 7.26). This suggests that the dominant did not rely on the *recruitment* glance to walk towards the cucumber.

Cross Correlation, Pair 2 Unequal Rewards: When the Subordinate Uses *Recruitment* Glances Towards the Cucumber, Does the Dominant Walk Towards the Cucumber?

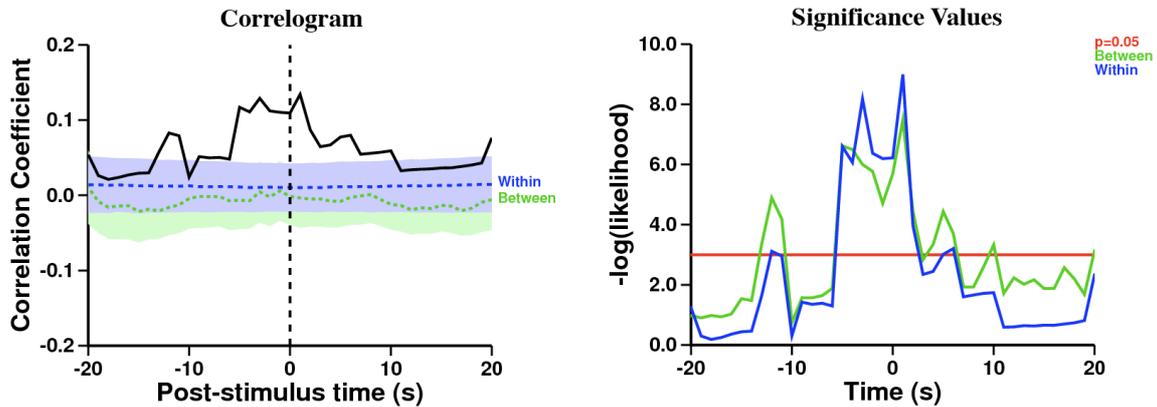


FIGURE 7.26: Referent behaviour: subordinate gazes towards the cucumber for two seconds, while stopping locomotion for five seconds. Target behaviour: dominant walking towards the cucumber. Before, during, and after the subordinate used *recruitment* glances, the dominant walked towards the cucumber significantly more than expected from the within-trial shuffled control (peak at time= +1, $r = 0.1830$, $n = 1781$, $-\log\text{-likelihood} = 8.9944$, $p < 0.05$).

On the few occasions that the subordinate used *recruitment* glances towards the banana, they cued the dominant to walk towards the hidden banana; but the dominant was already walking towards the cucumber when the subordinate *recruited*.

VI. Discussion: Pair 2

On the rare occasion that the subordinate did use *recruitment* glances towards the banana, the dominant walked towards the banana immediately, indicating that the *recruitment* glance was a very strong cue influencing the dominant to approach. Perhaps the subordinate's *monitoring* glance before walking towards the banana was used to check on whether the dominant was looking or moving towards the banana, and if not, the subordinate then started walking. This, however, did not prevent the dominant from using some other cue, most likely the subordinate's movement, to walk towards the banana.

The subordinate used both *monitoring* and *recruitment* glances while walking towards the cucumber: the dominant walked towards the cucumber before, during and after these glances, suggesting that it was not the visual cue itself that motivated the dominant to follow.

It seems as though the subordinate realised the effects of her gaze alternation and movement pause. The effect of her rare *recruitment* glance towards the banana was strong in prompting the dominant to approach; it is possible that the subordinate flexibly used *recruitment* glances towards the cucumber as an intentional manipulation of the dominant's behaviour. Subordinate Reinette's tactic may have been effective, as she *recruited* the dominant first to the cucumber on nine trials: and on four consecutive trials (11-14) the subordinate subsequently left the area where the cucumber was hidden and retrieved the banana for herself, without the dominant following. Since we know that the subordinate preferred banana to cucumber, her behaviour here appeared to be an example of tactical deception, specifically of deception by attraction: the subordinate used misleading tactics by moving towards an object of interest (the cucumber) which functioned to take the dominant's attention away from the subordinate's goal (the banana).

VII. Discussion for Both Pairs

Subordinate chimpanzees in both pairs used *monitoring* glances only before (but not during or after) walking towards the hidden banana, and they did not *recruit* towards the banana. Both dominant competitors walked towards the banana before and after the subordinate used *monitoring* glances towards it, and on the occasion that the subordinate of Pair 2 did use a *recruitment* glance, the dominant walked towards the banana. While the subordinate of Pair 1 used *monitoring* glances towards the cucumber only before walking towards it, the subordinate of Pair 2 *monitored* before and after she began walking towards the cucumber. One subordinate *recruited* her dominant opponent towards the cucumber, and the dominant walked towards the cucumber before and after the subordinate used either type of glance towards the cucumber, suggesting that the glance cues were not essential to inform the dominant of which direction to walk.

If we presume that the desired outcome of a *recruitment* glance, but not a *monitoring* glance, is for the opponent to walk towards the gazer and the destination, then these results support the hypothesis that the subordinates should use *recruitment* glances when walking towards the less-preferred cucumber. The results do not, however, support the prediction that

the subordinates should use *monitoring* glances while walking towards the banana. Despite the fact that the subordinates did not alternate gaze between the dominants and the hidden banana while walking towards it (as they did towards the cucumber), the dominants were still motivated to follow and search. It is possible that the subordinates learned that their *monitoring* gaze alone (i.e., without a pause in locomotion) was a sufficient cue eliciting the dominant opponents to follow towards the cucumber, and thus did not use it as frequently while walking towards the banana. *Monitoring* glances encouraged dominants to follow, and it seems that a pause in movement to *recruit* was an additional cue that one subordinate used flexibly and intentionally when walking towards the cucumber only.

The chimpanzees in this study used two different types of gaze alternation, *monitoring* and *recruitment* glances, and though the outcome of the dominant approaching the bait was not essentially different when the subordinate used either type of gaze, the results raise the question of whether the subordinates used these cues intentionally. Tomasello and Call (1997) define an action as intentional if a goal is implied and the agent exhibits behavioural flexibility in reaching a goal. The subordinate in Pair 2 used the tactic of *recruiting* the dominant towards the cucumber, and was successful in later retrieving the banana for herself on several of those trials. The subordinate of Pair 2 appeared to treat the cucumber as a 'decoy' reward: she preferred it less, and with the learned expectation that her dominant opponent would pick up an uncovered bait, the subordinate specifically *recruited* the dominant towards the cucumber, but not the banana. Thus, by attracting the dominant to the cucumber (by looking and leading), the subordinate was able to achieve her proximate goal of occupying the dominant in a search, and her ultimate goal of obtaining the banana without the dominant's interference (Byrne & Whiten, 1990). This intentional pause while gazing towards the cucumber functioned to tactically deceive the dominant. This is similar to reports from other informed individuals tested in this paradigm, that searched for smaller rewards or searched in locations where no reward was to be found (Menzel, 1974; Coussi-Korbel, 1994; Hirata & Matsuzawa, 2001; Ducoing & Thierry, 2003; Bugnyar & Kotrschal, 2004).

Chimpanzees in the wild use multiple different cues to coordinate group movement, such as buttress drumming (Reynolds & Reynolds, 1965; Boesch, 1991a; Arcadi et al., 1998) and vocalisations such as pant hoots (Goodall, 1986; Mitani & Nishida, 1993). Squirrel and capuchin monkeys have vocalisations specific to group movement (Boinski, 1991, 1993).

Hamadryas baboons observe and follow dominants' intention movements (Kummer, 1968). While physical and vocal cues are well documented for many species, forest visibility may prevent quality observation of visual cues, such as *monitoring* and *recruitment* glances. Data for this study were collected in captivity with high visibility, and the results highlight the chimpanzees' use of visual cues in addition to physical cues, though no vocal cues were recorded. Further research in natural conditions is necessary to elucidate whether visual cues are used by, and are useful to, chimpanzees in a dense forest environment.

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I. Discussion

Using the informed forager paradigm, I investigated whether chimpanzees follow opponents' gaze to modify their own competitive tactics. The chimpanzees in my study behaved similarly to subjects in previously published studies with a variety of primate and non-primate species: as the interaction developed, dominant subjects followed their subordinate opponents closely to scrounge on food, and subordinate subjects reacted to scrounging by delaying their approach to, or by taking an indirect route to, the food (Menzel, 1974; Coussi-Korbel, 1994; Hirata & Matsuzawa, 2001; Held et al., 2002; Ducoing & Thierry, 2003; Bugnyar & Kotrschal, 2004). Additionally, when a less valuable food was also hidden, the subordinate of Pair 2 consistently led her dominant competitor to it first, before turning to retrieve the preferred item (as in Menzel, 1974).

The purpose of this research has not been to determine what chimpanzees know about others' states of knowledge, but rather *how* they use different physical movement types and different gaze types to modify their competitive tactics in the informed forager paradigm.

A. Chimpanzees follow physical movement to exploit each other's foraging success, a demonstration that cross correlations are appropriate for analysing behavioural data

My data on chimpanzee movement following supports previous narratives of subjects' behaviour in this paradigm: namely that dominants physically follow informed subordinates to exploit their privileged knowledge, and especially that the dominants *change* their following tactics as the interaction develops (Chapter 5). The dominants in this *Competition* experiment acted to exploit the foraging success of their subordinate competitors by using three different types of movement (following by *approaching*, following in the other's *footsteps*, and following by *convergence*). This allowed them to arrive at the location of the hidden bait in order to scrounge, and to walk ahead of their opponent along the same path to arrive at the food first in order to take it. The dominants evidently had to learn to use these following tactics over several trials. Subjects did not use the same movement or gaze types as in the *Competition* in various control conditions in which they had different states of knowledge (*Full Knowledge, No Knowledge, No Bait, No Knowledge*); this suggests that their differential use of movement and gaze types reflects their changed states of knowledge. An analysis of a subject's movement or gaze behaviour cannot prove that 'she knew that the other knew where the food was hidden,' but it can provide insight into how she developed a

particular competitive tactic based on prior events such as a success or a loss, or a current event such as how her opponent behaves.

I have used cross correlations to show quantitatively what previous published studies have merely described as happening (Menzel et al., 1974; Coussi-Korbel, 1994; Hirata & Matsuzawa, 2001; Ducoing & Thierry, 2003, 2004; Held et al., 2002; Bugnyar & Kotrschal, 2004), by highlighting the nuances in behaviour that might not otherwise be exposed. It was possible to achieve this level of detail by dividing my data set into three distinct phases as the competition developed, and by defining “following” in three different ways. A comprehensive analysis of subjects’ following behaviour in this paradigm has the potential to reveal which behavioural patterns or contingencies motivate subjects to change their own behaviour in response to others’ behaviour, thus statistically demonstrating what Menzel originally described as “continuous feedback” between subjects (Menzel, 1974, p. 134).

B. Chimpanzees follow conspecific gaze, and gain information regarding the location of hidden food from gaze-following interactions

As reported by Tomasello et al. (1998) and Hare et al. (2000), chimpanzees are able to follow the gaze of a conspecific, and data from my study lends additional support to this claim (Chapter 6). While all four subjects did follow the gaze of their opponent, a consistent pattern emerged that contradicted predictions from Chance’s (1967) social attention hypothesis: in my experiments, the dominant followed the subordinate’s gaze more than the reverse. I propose that in this experimental setup, in which only the subordinate has privileged knowledge of the location of a hidden food item, the dominant follows the subordinate’s gaze primarily in order to seek information from her. Moreover, dominants did not follow the subordinates’ gaze when they had seen the food hidden.

Previous studies on chimpanzees’ understanding of gaze, as indicative of the mental state of attention, found that chimpanzees were largely unable to use (human-given) gaze cues to locate food hidden under one of two opaque cups, despite exposure to hundreds of trials (Povinelli et al., 1990; Call et al., 1998; Itakura et al., 1999). Contrary to those findings, Hare et al. (2000, 2001) reported that chimpanzees were able to understand that ‘seeing’ leads to ‘knowing,’ and that during food competition subordinate subjects retrieved more food that was not visible to a dominant competitor than food that was visible to both. In support of the competitive hypothesis put forth by Hare (2001) and Hare and Tomasello (2004), which suggests that chimpanzees are more likely to show their abilities in a natural

context (see also Matheson et al. 1998), the dominant chimpanzees in my study were able to follow their conspecific opponent's gaze and use information gained from the gaze interaction to modify their own movement towards the hidden bait (Chapter 6). For example, dominant Rita followed subordinate Missy's gaze while *converging*, indicating some ability to geometrically follow Missy's gaze, possibly around barriers in their enclosure (Tomasello et al., 1999; Okamoto-Barth et al., 2007), and then adjust her own movement to walk towards Missy's assumed destination. Dominant Georgia was very successful in following Reinette's movement and gaze, and then walking ahead of her along the same path to arrive at the food first.

By defining two types of gaze following, based on following *static* or dynamic (*onset*) cues, I contribute to the debate over what may elicit a gaze following interaction. Several studies have shown that in this circumstance, cues from the direction of the head override those from the body (Hietanen, 2002; Kaminski et al., 2004; Seyama & Nagayama, 2005; Shepherd & Platt, 2008). Although my definitions of the two types of gaze following did not necessitate that the subject's direction of gaze was incongruent with her body orientation, my data nevertheless support this: when a subject's direction of gaze (originating from her head orientation) was incongruent with her body direction, her opponent did follow her gaze (Chapter 6). Perhaps a change in gaze direction with a motion cue, such as a gaze onset, indicates that something has actively captured a subject's attention, while a static cue, rather than suggesting intense fixation on an object generally only indicates that the subject is passively viewing a scene, unless paired with other physical cues (Paukner et al., 2007). Tomonaga (2007) conducted a series of gaze-tracking experiments with chimpanzees, and presented a quasi-dynamic cue: a series of two photos of a human demonstrator, first a forward facing head with eyes gazing in one direction, followed by a profile view of the head facing towards the same direction. Tomonaga found that this presentation triggered significant cueing effects towards a target that then appeared on the side indicated by the cue, whereas single still images of averted gaze or faces in profile (as well as non-facial cues such as arrows) did not elicit the same shift in gaze direction. Tomonaga's study demonstrated that dynamic cues could potentially carry more signal value than static cues. My results on following gaze onset, however, are less clear: each subject behaved differently. One dominant followed her competitor's gaze onset during the *Competition* and the *No Knowledge* control condition, and the other dominant followed her competitor's gaze onset in

only the *Full Knowledge* control. One subordinate followed her opponent's gaze onset in every condition, whereas the other subordinate did not follow her opponent's gaze onset in any condition. While following static gaze seemed to be the same for both chimpanzees in the subordinate position, and the same for both chimpanzees in the dominant position, the results of their following gaze onset did not follow a consistent pattern. More research into whether the dynamic motion involved in a head-turn elicits gaze following more effectively than a static gaze cue is needed in a naturalistic context.

C. Chimpanzees can use gaze flexibly and intentionally

As discussed above, chimpanzees can use the direction of others' gaze to modify their own behaviour. Kano and Tomonaga (2009) suggested that chimpanzees have "active, voluntary control of gaze" (Kano & Tomonaga, 2009, p. 1953). In addition, Gómez (1991, 1996) and de Waal (2001) described instances in which great apes have used their gaze in a deictic manner to capture and redirect the attention of a human. Complementary to these studies, the results from my two experiments, especially the *Unequal Rewards* experiment, lead me to propose that chimpanzees can also use their own gaze intentionally to modify the behaviour of conspecifics. They may do this in various ways, ranging from not gazing towards a target in order to withhold information from others, to alternating gaze between a target and another individual while pausing in movement to *recruit* the other towards the target.

1. Withhold

Towards the end of the *Competition*, the subordinates acted to avoid the dominant's exploitation pressure, in the form of close following and scrounging, by pausing in their movement towards the bait, and additionally by not gazing towards the bait when they did pause (Chapters 5 and 6). This indicates that the subordinates were capable of delaying their own immediate desire to retrieve the food, and also of acting to prevent their competitor from retrieving the food. When the subordinates did not give any movement cues towards the bait, the dominants could no longer follow; and when the subordinates did not give any visual cue towards the bait, the dominants could not gain any further information regarding its location. Therefore, the subordinates used the (lack of specific) direction of their own gaze to manipulate the dominants, effectively preventing them from finding the bait.

2. Recruit

In the *Unequal Reward* experiment, the goal of my analysis was to detect whether a single behaviour—such as gaze alternation—may have multiple different functions when applied flexibly in different situations. Though these scenarios appear similar on the surface, there are subtle differences, such as a pause in movement that can reveal how a subject employs a tactic in order to achieve a goal. I found that one informed subordinate subject flexibly used *recruitment* glances to invite her dominant competitor to follow to the location of the hidden cucumber but not the more valuable banana (Chapter 7). This suggests that she was capable of using her gaze alternation and movement pause to direct the dominant's attention to a specific item of interest in their enclosure, and treated the cucumber as a 'decoy' bait. In doing so, the subordinate was able to attract the dominant to walk towards that location. While the dominant was occupied with retrieving the cucumber, the subordinate often turned around to search for the banana. Therefore, the subordinate used her gaze to manipulate the dominant into taking a less preferred bait, and in some cases this effectively served to occupy the dominant long enough for the subordinate to obtain the more valuable bait.

D. New statistical method opens the possibility to better understand competitive tactics

Cross correlations can show broad relationships between subjects, such as various movement following patterns and how they gradually change over time. Cross correlations can also pinpoint specific contingencies, such as the relationship between looking at the opponent and then immediately gazing towards the same direction as the opponent. The exploratory method of my analysis can reveal any number of relationships where one might not have thought to look. For example, I suspected that the subordinate in Pair 2 in the *Unequal Rewards* experiment used gaze alternation in different ways while approaching the banana or the cucumber; it was not until I sifted through different combinations of variables that I was able to find that the difference in her behaviour was due to a brief pause in her locomotion. Commonalities between both pairs I tested indicate underlying patterns that are common to chimpanzee behaviour and perhaps also common to the informed forager paradigm: my analysis of behaviour that may be interpreted as tactical deception revealed that both subordinates stopped walking and stopped gazing towards the bait in order to withhold information.

1. Problems to address

As with many studies on animal behaviour, and tactical deception in particular, obtaining a large enough sample size remains an issue. Though the Yerkes National Primate Research Center houses 22 chimpanzees, only four participated in my study, due to logistical constraints and non-participation (Chapter 3, appendix to Chapter 3). There were several reasons for non-participation: the only male that was tested was very passive in the ‘dominant’ role, and always allowed his female partner to take the food, and was therefore removed from the study (see appendix to Chapter 3). Other females could not be separated, even briefly, from group mates. One-on-one competition appeared too stressful for others. A larger, more diverse subject pool would be able to provide more insight into differences in behaviour due to ontogeny, age/sex class, or due to other reasons. Another way to increase sample size would be to continue testing the same pairs for more trials. By coding behaviour on a one-second time scale, I have managed to expand a limited number of trials into a sufficiently large data set to run the cross correlation analysis properly, though additional trials would increase the robustness of the analysis, especially for the control conditions in which only four trials were conducted.

II. Future Directions

By analysing data on tactical deception using this statistical method, it is possible to reveal underlying patterns that may be common to some or most acts of deception, so as to provide a better framework for designing and analysing future studies. Though the study of tactical deception is fraught with single-instance records that are entirely context-dependent, an experimental setup such as the informed forager paradigm allows one to collect and code numerous instances of possible tactical deception involving the same individuals, whose experimental history and social interaction outside the experiment are well known, in order to compile a larger set of records from which to draw conclusions. As McGrew (2004) advocates, “The lesson here is: report everything of interest clearly and precisely in print, to spur others. Then, replicate, replicate, replicate. The plural of anecdote *is* data” (McGrew, 2004, p. 176).

III. Conclusion

I have introduced a new method of statistical analysis, cross correlations, that has enabled me to examine behavioural patterns quantitatively that previous authors have only been able to describe in narrative form. In the informed forager paradigm, a subject's actions are often contingent on her opponent's actions, and the behaviour of both changes over time as they react to one another's competitive tactics. Similar to previous studies, the dominant chimpanzees in my study exploited the foraging success of informed subordinates by using three movement tactics: follow by *approaching*; follow in the other's *footsteps*; and follow by *converging*. Subjects' differential use of movement types in different experimental conditions reflected their changed states of knowledge.

Dominants were able to gain information regarding the location of the hidden bait by following informed subordinates' gaze. Using the direction of others' gaze to modify their own behaviour is already described in chimpanzees; I propose here the dominant followed the subordinate's gaze in order to seek information from her. Consequently, dominants did not follow the subordinates' gaze when they had seen the food hidden. While following *static* gaze showed a consistent pattern for dominants and subordinates, this was not the case for following gaze *onset*. More research is needed in a naturalistic context into whether the dynamic motion involved in a head-turn elicits gaze following more effectively than a static gaze cue. Results from the subordinates' efforts to avoid the dominants' exploitation lead me to propose that chimpanzees can intentionally use their own gaze to modify the behaviour of other conspecifics, either by withholding or recruiting.

An experimental setup such as the informed forager paradigm paired with the new statistical tool—cross correlations—allows one to contribute additional records of tactical deception so as to find commonalities among them.

The development of cross correlations for use in behavioural studies has brought to light the most detailed picture of how chimpanzees compete and employ different movement and gaze following tactics in the informed forager paradigm. This method, and the results presented here, will add to the fields of ethology and psychology a better understanding of gaze following in relation to information acquisition, how gaze cues can be used to modify one's own competitive tactic, and how gaze can be used to manipulate others' behaviour.

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Appendix 1: Ethics Proposal

This appendix includes details of an email exchange between myself and Elma Stanage, the Home Office Liaison Officer, my point of contact with the St Andrews Animal Welfare Ethics Committee.

February 26, 2009

Dear Elma Stanage,

I would like to submit another proposal to work with chimpanzees. In December you approved my study with capuchin monkeys, and this proposal you will find very similar in methodology. The dates I have listed are to be confirmed by the field site, but in any case I plan to dedicate one year to the project. I will update you with any changes.

Thank you,

Katie Hall

Ethics Proposal

1. **Name.** Katie Hall
2. **Status.** First year PhD in Psychology at University of St Andrews
3. **Supervisor.** Professor Dick Byrne
4. **Dates.** March 2009 – March 2010 (TBC)
5. **Project title.** Do Chimpanzees Have “Shifty Eyes”? Investigating the Cooperative Eye Hypothesis
6. **Subjects.** Two socially housed groups each of 12 chimpanzees at the Yerkes National Primate Research Center Field Station.
7. **Nature of study.** This study is an informed forager paradigm. It is experimental and observational. It involves giving access to privileged knowledge of the location of a hidden food item to one subordinate individual, then allowing her to compete with a more dominant individual to obtain the food. The Yerkes Field Station has a large outdoor enclosure, and an indoor space divided into four individual-sized cages and a larger room known as the Cognition Room.

In order to carry out my project, I will move the group of chimpanzees into the Cognition Room, and then separate a subordinate individual into a smaller cage to inform her of the location of hidden food. A dominant individual will also be separated into a smaller cage, but without visual access to the baiting procedure. I will have ten PVC tubes, each painted a different color for easy recognition, and I will hide food in a different tube on each trial. I will place all ten tubes in the outdoor area before the competition, and release both competitors outside at the same time. Ten tubes should be too many for an ignorant chimp to search on his own, but not too many that a knowledgeable chimp couldn't keep track of the baited one (or two in later trials).

During the competition, data collection will be purely observational, videoing the chimpanzees' behavior so that I can track who is watching whom, as well as scoring who ultimately obtains the food reward.

Chimpanzee subjects will not be deprived of food; the food reward will be a special treat, such as an apple.

The focus of the research is to determine (1) whether informed foragers can benefit from their privileged knowledge; (2) whether non-informed individuals can 'read' the

knowledge of the informed individual, and thus use their dominance to benefit from it; and if so, (3) whether informed individuals can counter this exploitation in any way, for instance by deceiving the exploiter. Video collected from this experiment will be analyzed in the relation of head orientation to body movement during competitive interactions, in order to discern the intentions of individuals engaged in competitive interactions.

8. **Schedule.** March 2009—March 2010. At the beginning of the study, I will determine dominance ranking among all possible pairs of chimpanzees in a food competition that will take place in the indoor enclosures. I will spend a few hours each day training individual subjects to recognize the ten colored tubes that will be used for concealing food rewards, and to choose the one in which they witnessed me place the food. Also as part of this Experiment, I will bait two tubes, one with a better reward than the other (half versus whole fruit, or two different items with clear preference value). I will test that each subject can remember the hidden location of the two rewards, and that when given a choice, they consistently choose the better reward first.

Then, I will introduce the element of competition in Experiment Two. I will first bring all chimpanzees into the Cognition Room to be held during a trial. The two competitors will be chosen to each enter their own holding cage, and will be in adjacent cages with visual access between them. I will set up an opaque panel so that only the subordinate subject can watch me bait one PVC tube; because the cages have visual access between them, the dominant has the opportunity to see that the subordinate has seen the baiting (but cannot see the baiting himself).

I will leave the testing room with a bucket containing all ten tubes, go up to the observation tower, and throw the tubes into the outdoor area. Then, I will release both competitors outside at the same time. I will have one stationary camera to film the scene from the tower (with a starting frame on the doors to capture any social interactions between dominant and subordinate as they begin to compete), and one camera on the ground at an appropriate location. I will describe head orientation versus body movement, and consider gaze following as further evidence that chimpanzees can use visual information to exploit the foraging success of others.

In one control condition, I will show both competitors as I bait the food to determine the influence of the dominant on the subordinate's behavior. In another control, neither will see the baiting process and therefore must search for food as in a natural foraging situation.

For the second part of Experiment Two, I will hide two rewards in different tubes; one reward will be better than the other (quantity or quality). The subordinate will be released a few seconds ahead of the dominant into the outdoor area. If the subordinate understands that the dominant is ignorant of the second reward, she should go directly to the tube with the smaller reward before the dominant, because she can later return to the larger reward, and obtain both foods (and if the dominant steals the first reward, not much has been lost).

In a control condition, the subordinate will see both tubes baited, and the dominant will have the opportunity to watch as I bait the smaller reward only, to show that the dominant will not follow the subordinate if he has information of his own.

For the third experiment, both the dominant and subordinate will watch as I bait one colored tube. Then I will raise the opaque partition so that only the subordinate can see as I either remove and replace the food in the same tube (lift), or remove and place the food into a new container (shift). Once again, I will carry the bucket of colored tubes out of the testing area and throw the tubes from the tower into the outdoor area. Both competitors will be

released at the same time. If the subordinate understands that his competitor did not see the final hiding location of the food, and therefore expects the food to be in the original tube, the subordinate should not hesitate to approach the correct tube while the dominant searches elsewhere.

In a control condition, both competitors will see the food's final hiding location.

9. Ethical considerations. This study aims to observe how chimpanzees interact in naturalistic social settings. Chimps foraging in the wild often experience inequities including knowledge of where food is, how to access it, and occasionally experience loss of food to dominant individuals. I expect this to happen during the course of the study, though this is no different from what the chimps experience on a daily basis. I want to focus on observing the intelligent behavioral tactics that develop to reduce food loss.

10. Welfare of animals. I will have no physical contact with the chimpanzees. Subjects will participate on a self-selecting basis: they will be rewarded for coming when they are called, and only positive reinforcement will be used during training. Individual subjects might become stressed when separated from their social group; however, these chimpanzees have participated in numerous individual cognitive studies, and beyond being accustomed to occasional 'alone time,' are enthusiastic to do so. Individuals will benefit from the behavioral enrichment of searching for hidden food and exploring the outdoor enclosure.

February 26, 2009

Many thanks for sending me this proposal Katie. I will circulate to AWEC members and get back to you with their comments as soon as possible.

Regards
Elma

March 5, 2009

Dear Katie

AWEC members were pleased to receive your proposal for comment. For their information I would be grateful if you could respond to the queries they raise below -

- Thank you for forwarding Katie's proposal for her PhD study. She says that the particular group of chimps she will be using have participated in numerous cognitive studies and were keen to do so. I wonder if this habituation will have any significant impact on the results or can it be assumed from previous studies that there won't be any marked difference in the response of these chimps to those who are in the wild. I am assuming that she is mainly interested in what happens in the wild, otherwise what value is she specifically seeking here with chimps already in the research pool? It seems that quite a lot is known about their behaviour already. She has written a clear outline of what she wants to do; there doesn't appear to be a major welfare issue other than potential stress which she says would be similar to what would happen in the wild. I don't think I have any other questions; I am just curious as to whether this habituation could have an effect on the outcome

- I have read through the proposed research and had a look at the web site for the Yerkes Primate Research Centre at Emory University in Atlanta which is a large centre dedicated to this type of research as well as much other Primate work. I have no problem with the research and would imagine this is a wonderful opportunity for Katie to gain experience working in such a place. It would be interesting to hear the results of this particular research sometime in the future.

I look forward to hearing from you shortly.

Regards
Elma

March 11, 2009
Hi Elma,

Im sorry it seems I have overlooked your email. In response to your questions, I doubt that the chimpanzee subjects' previous experience in cognitive studies will have any effect on their behavior, because I am trying to experimentally manipulate situations that mimic those that the animals experience either in the wild, or on a daily basis, while foraging for food. The difference is in which individuals have knowledge about the location of the food.

In terms of comparing captive to wild chimps, I can say that it would be nearly impossible to manipulate knowledge states in wild chimps in the same way I propose here. Furthermore, the setup of the Living Links Field Station is well-suited for video recording the subjects' gaze following interactions, which would be obstructed by foliage in the forest. But I do expect the captive chimps to act in a similar way as would wild chimps: a subordinate would wish to avoid punishment or food-stealing by a dominant, and it has been observed by Jane Goodall (and others) that subordinates often conceal information about hidden food until a dominant is distracted before approaching the hidden food.

My contribution to the field is discovering the mechanism that links acquisition and application of knowledge in order to deceive another, and I hypothesize that chimpanzees use gaze following to do this.

I hope this helps,
Katie Hall

March 12, 2009
Many thanks for answering the queries raised. I will pass this on to the AWEC members.

All the best in your research.

Regards
Elma

Appendix 2: Ethogram

Subjects		Behaviors				Modifiers	
Subject Name	Behavior Name	Behavior Type	Modifiers	Modifier Name			
Missy	NEW Change Direction	Point Event	<Click here to add Modifier groups>	Up	u		
Katie	Change Direction	Point Event	<Click here to add Modifier groups>	Down	d		
Tara	Not Visible	x	State Event	Chimp (Nominal, Optional)			
Reinette	No Locomotion	n	State Event	● Closer	t		
Rita	Walk	w	State Event	● Further	a		
Socko	Run	r	State Event	Bait (Nominal, Optional)			
Donna	Climb	c	State Event	● Towards	l		
Anja				● Away	f		
Georgia				Direction (Mutually exclusive, Nominal, Optional)			
				● Left	e		
				● Right	r		
				Food (Mutually exclusive, Nominal, Must be scored)			
				● Banana	n		
				● Cucumber	m		
				● No Reward	w		
				Moving towards (Mutually exclusive, Nominal, Must be scored)			
				● Q1	1		
				● Q2	2		
				● Q3	3		
				● Q4	4		
				● 0	0		

BEHAVIOURS

Locomotion

- **Change Direction:** Any deviation greater than 30 degrees from straight-line path. Also code when changing between modes of locomotion (walk-climb, climb-run, (but not walk-run, unless direction actually changes, etc). Code for any body-orientation shift of 90 degrees or more when not locomoting. Do not code if movement following “No Locomotion” is in the same direction as before the pause. If a subject changes direction while moving, it is sometimes also necessary to re-code that behaviour for its modifiers; for example “Walk, towards chimpanzee—Change Direction—Walk, away from chimpanzee.”
- **Not Visible:** Code when subject is off-camera, inside, or is obstructed by something in the environment for more than 1 second. Always code with “Neutral.”
- **No Locomotion:** Sitting, lying down, or a pause in locomotion for more than 1 second.
- **Walk:** Code from first step, but do not code if subject does not take more than 2 steps (scoot, false start). Modified by “Chimpanzee” and “Bait,” but does not require that both be coded (for example, if bait is found, don’t code that modifier).
- **Run:** Same as “Walk.” Code as “Run” if increased speed/bounce in gait. Subjects usually speed up into a run from walking, so code first faster/bouncier step. Modified by “Chimpanzee” and “Bait,” but does not require that both be coded (for example, if bait is found, don’t code that modifier).
- **Climb:** Climbing on ladders, poles. Code as “Walk” if on platform levels (with “Change Direction” at transition). Modified by “Climb,” which must be coded, and “Chimpanzee” and “Bait,” but does not require that both be coded (for example, if bait is found, don’t code that modifier).

Bait Directed

- **Approach within 1m:** Code when either subject is within 1m radius of food location. Modified by “Food,” which must be coded.
- **No Bait Directed:** Not exhibiting behaviour related to food (no active search, no carry, eat, etc). Usually prefer to start/stop other behaviours in this category, but there are cases when food is immediately present and a subject shows no interest, in which case, “No Bait Directed” should be used.
- **Search:** Active search for food (food may or may not be present). Often involves looking un/under objects in compound. Code from first look/touch of object. Stop coding when gaze shifts. Modified by “Food,” which must be coded.
- **Seize food:** Instant that food is picked up. Modified by “Food,” which must be coded.
- **Carry:** Food is carried in hand or mouth. “Carry” can occur before or between bouts of eating. Modified by “Food,” which must be coded.
- **Eat Food:** Actively eating food. Often involves gazing at “Bait.” Modified by “Food,” which must be coded.

Gaze Behaviour

- **Neutral:** Head is in a neutral orientation with respect to shoulders/body AND there is no “Chimpanzee” or “Bait” in direct line of sight. Always code when subject “Not Visible” (ok to code again if “Neutral” already active).

- Bait: Subject is oriented towards a food item. Can (but not necessarily) occur with “Approach within 1m,” “Search,” “Seize Food,” “Carry,” “Eat Food.” Modified by “Food,” which must be coded.
- Chimpanzee: Subject is oriented towards another chimpanzee.
- Elsewhere: Head deviates 30 degrees or more from neutral position AND there is no “Chimpanzee” or “Bait” in direct line of sight. Modified by “Direction,” which must be coded.

Proximity Between Chimpanzees

- Close within 2m: Always code for subordinate only. Estimate distance.
- Not Close: Always code for subordinate only. Estimate distance.

Dominant Distance to Food

- Closer than Sub: Always code for dominant only. Distance to food is relative to partner.
- Further than Sub: Always code for dominant only. Distance to food is relative to partner.
- Neither: Always code for dominant only. Code immediately after “Seize food.”

Social Interaction

- No Social Interaction: Usually prefer to start/stop other behaviours in this category.
- Peer: Subject very closely watches as partner eats food. Can occur with “Chimpanzee” or “Bait.”
- Beg: Open, palm up gesture in food context.
- Threat: Piloerection, swagger, arm flail, or any agonistic interaction (fight).
- Greet: Pronated wrist, pant-grunt, affiliative interaction.

Dominant Visual Access to Subordinate

- Yes: Dominant’s view of subordinate is not obstructed (though dominant may not be oriented towards subordinate)
- No: Dominant’s view of subordinate is obstructed. Often coded with “Not Visible” and “Neutral.”

Gaze Towards Bait

- Gaze: Code for both subjects when their gaze is towards the location of the hidden bait. Modified by “Food.”

Absolute Direction

- In Q1: Subject is currently in Quadrant 1 (Quadrant includes space underneath the Office Tower, the metal monkeybars, the hammock under the climbing structure). Modified by “Moving Towards.”
- In Q2: Subject is currently in Quadrant 2 (Quadrant includes space by Lixit, to the telephone pole on the back side of the climbing structure, the left half of the climbing structure). Modified by “Moving Towards.”
- In Q3: Subject is currently in Quadrant 3 (Quadrant includes space closest to ‘Cognition Room,’ none of the climbing structure. Modified by “Moving Towards.”
- In Q4: Subject currently in Quadrant 4 (Quadrant includes space underneath the Viewing Tower, the stairs and telephone pole up to the central climbing structure, and the culvert on the left side of the enclosure. Modified by “Moving Towards.”

- No Info: Subject is inside; not in any quadrant. Modified by “Moving Towards.”

Absolute Gaze

- LookQ1: Subject is gazing towards Quadrant 1, including objects on the ground within Q1.
- LookQ2: Subject is gazing towards Quadrant 2, including objects on the ground within Q2.
- LookQ3: Subject is gazing towards Quadrant 3, including objects on the ground within Q3.
- LookQ4: Subject is gazing towards Quadrant 4, including objects on the ground within Q4.
- NoInfo: Subject’s direction of gaze cannot be determined.

MODIFIERS

- Climb: Up or Down.
- Chimpanzee: Whether the subject is moving Closer to or Further from their partner.
- Bait: Whether the subject is moving Towards or Away from the bait. Do not code after the bait has been found. Bait always refers to Banana.
- Direction: Left or Right.
- Food: Banana, Cucumber, or No Reward. Code “No Reward” when subject is searching where nothing is hidden.
- Moving Towards: Q1, Q2, Q3, Q4, 0. Code “0” when subject is not moving.

Appendix to Chapter 3: Experimental Methods for Tube & Bucket Training

I. Introduction

II. Tube Training Methods

- A. Subjects
- B. Setting
- C. Behavioural Recording
- D. Apparatus
- E. Experimental Design
- F. Procedure for each condition
 - 1. *Banana only*
 - 2. *One paper*
 - 3. *Two papers*
 - 4. *Rearrange*
 - 5. *In/out*

III. Results

- A. Individual results
 - 1. *Missy*
 - 2. *Tara*
 - 3. *Reinette*
 - 4. *Katie*
 - 5. *Tai*
 - 6. *Barbie*
 - 7. *Julianne*
- B. Pooled data from FS1 and FS2
- C. Dropping Tubes into the Enclosure

IV. Short Discussion

V. Bucket Training Methods

- A. Subjects
- B. Setting
- C. Behavioural Recording
- D. Apparatus
- E. Experimental Design
- F. Procedure

VI. Results

VII. Short Discussion

VIII. Conclusion

I. Introduction

In some previous studies in the informed forager paradigm, food was hidden among numerous containers (buckets, boxes, cups) placed in the subjects' living area specifically for the duration of the study (Coussi-Korbel, 1994; Held et al., 2000, 2002, 2005, 2010; Hirata & Matsuzawa, 2001; Bugnyar & Kotrschal, 2004). Hirata and Matsuzawa (2001) report that the dominant individual in their study gained information from the subordinate regarding her direction of movement, and because the dominant was familiar with the experimental boxes, she would run ahead of the subordinate to the container in her line of travel (p. 290). It was very clever of the dominant to gain information and take advantage of the subordinate in this way, but it made it difficult for the subordinate to win on any given trial after the dominant learned where the five containers were located in their enclosure.

For the purpose of the current experiment, I did not want the experimental setting to be too easy for the dominant to assess where the food was hidden without genuinely searching for it; as well, there should more opportunity for the subordinate to win and stay motivated to participate. Rather than hiding the food at specific fixed locations, I hid a banana in one of five differently colored PVC tubes, and then threw them randomly into the enclosure from the Viewing Tower. The subordinate subject would be shown which of the tubes was baited so she would have a search image: she would know *what* to look for, but not exactly *where* to look. This would make it more difficult for the dominant to immediately assess the food's location based on the subordinate's direction of movement, since the subordinate would have to search as well, and may not give a cue indicating that she had found the correct tube. We assumed that the subordinate would avoid picking up empty tubes.

A study by Kanngiesser and Call (2010) showed that all great apes use feature and spatial cues in spatial memory tasks, but prefer to use feature cues (colour, shape, pattern) over landmark configuration when searching for hidden food. For the present study, we trained chimpanzee subjects to recognize and distinguish between the feature properties of five PVC tubes, and then the spatial properties of five buckets.

Chimpanzee subjects were trained to recognize and distinguish between five differently coloured and patterned PVC tubes, in preparation for the planned informed forager experiment. The original idea for the study was to lock all chimpanzees inside, isolate a subordinate chimpanzee, and inform her which one of the five PVC tubes was baited

with a whole banana; then the experimenter would throw all five tubes into the enclosure from the Viewing Tower. Throwing the tubes from the tower would minimize any risks associated with humans entering the chimpanzee enclosure in order to hide the food, and would reproduce a more natural foraging situation in which the subjects must search not only for the five tubes but specifically for the correct tube, rather than approach the tubes at a fixed location as in Hirata and Matsuzawa (2001). During the experiment, the informed subordinate would compete with an ignorant dominant to find the food.

The chimpanzees had success on the initial tube training, and learned to only choose the baited tube when confronted with a choice among five, in an indoor setting. Despite the subjects' early success in the tube training, I encountered problems when I threw the tubes into the enclosure; I expected the subject to pick up the baited tube first and ignore empty tubes. However, the subjects picked up every tube on every trial, and did not always choose the baited tube first. To account for this problem, I switched to a spatial cue, and trained the chimpanzees to associate each tube with a specific bucket at a fixed location on the perimeter of their enclosure. However, as with the initial use of the tubes, there was no cost associated with searching all five bucket locations, even after the food had been found on a trial, and so this method was abandoned as well.

II. Tube Training Methods

A. Subjects

Chimpanzees from both groups at the Yerkes Field Station were chosen based on their lower rank in the dominance hierarchy to participate in tube training. Only subordinate chimpanzees participated in tube training, to maintain their status as “informed,” whereas dominant partners were “ignorant” to the purpose of the tube as a hiding place for a desirable food item. The following mid- to low-ranking chimpanzees participated in the tube training: Katie, Reinette, Tara, and Missy from FS1; Barbie, Tai, and Julianne from FS2. All participation was voluntary, and other subordinates chose not to participate for various reasons, including fear of being locked in a cage alone, and neophobia towards the tubes. The subjects had to come inside, alone (or in a few cases, with a family member), in order to prevent observational learning of the task by other members of the social group.

B. Setting

During training, an individual chimpanzee was isolated into a familiar cage using positive reinforcement (verbal encouragement and small food rewards). In FS1, training and testing occurred in both the Bedroom area and the Cognition Room area. In FS2, training only occurred in the Bedroom area, and on occasion subjects in this group were trained in the presence of other non-participating chimpanzees to increase the subject's comfort level.

C. Behavioural Recording

All training sessions were video recorded using a Sony DCR-HC52 camera on a tripod. Subjects' tube choices were marked on a printed datasheet (see Section E, Figure 1 below) during the session, and verified on the videotapes afterward.

D. Apparatus

Chimpanzee subjects were trained to recognize and distinguish between five PVC tubes (12" length x 2" diameter). Each tube had a different colour and pattern for easy identification, discrimination, and to differentiate these tubes from those used by other researchers in previous studies in which each tube was exchanged for a reward, which would not be the case in the current study (Brosnan & de Waal, 2005; Brosnan et al., 2005; Bonnie et al., 2007; Horner et al., 2010). Each tube was assigned a number for randomization purposes. The tubes were presented to the subjects on a wire mesh carry cart with wheels.

TABLE 1: Tube description

Tube #	Description
1	Red with black bar
2	Yellow with purple stars
3	Green and gold vertical waves
4	Light blue with dark blue dots
5	Purple and white horizontal stripes



FIGURE 1: Tube photo

E. Experimental Design

Tubes were presented equally spaced on the wire mesh carry cart to the chimpanzees in blocks of five trials, and presentation was semi-randomized such that the order of tubes on the tray was never the same; each tube was baited an equal number of times, and all five were baited before any one was repeated; the baited tube appeared in a different position on the tray on each trial, and all five positions were used before repeating. No colour or position was repeated twice in a row between blocks of trials. Refer to Figure 1 for an example of the semi-random order of presentation.

TABLE 2: Datasheet with Tube order

BAIT	POSITION
2	42315
1	24315
5	32541
4	15324
3	31452
1	45321
4	23541
3	43215
2	13254
5	51243
3	42153
5	25134
4	41253
1	23145
2	41325

F. Procedure for each condition

During training, an individual chimpanzee was isolated into a cage, and presented with all five tubes equally spaced in the predetermined semi-random order on a wheeled wire mesh cart at the cage mesh. On each trial, an experimenter E1 picked up the tube to be baited indicated by the datasheet, lifted it to the subject's eye level to show that it was empty, baited it with a small slice of banana 0.75 cm thick, and set it back on the tray. In some conditions, pieces of crumpled paper were placed in the front end of the tubes to block visual access to the banana slice. Then the tray was pushed towards the cage so that the edge was flush with the cage mesh. Subjects could point through the cage mesh to indicate their tube choice, and were only allowed to choose one tube per trial. Choices were unambiguous, and E1 marked the subjects' tube choices on the datasheet. Choices were later verified by consulting the videotape of the session. Any ambiguous trials, trials in which the subject indicated no choice or more than one choice, or any trial that was incorrect due to experimenter error (failure to remove banana from the tube before beginning baiting on the next trial, so that two tubes contained banana slices) were excluded from the analysis. The subject was always rewarded for choosing the correct tube with the banana slice and verbal praise ("good job!"); if the subject chose incorrectly, E1 held up the empty tube to show her that there was no banana, and said "sorry, wrong one!" E1 then removed the banana from the correct tube and set it aside for another trial. After each trial, the tray was pulled back from the cage approximately one meter, emptied of all pieces of food and paper, and the tubes were rearranged in the semi-random order for the next trial.

I presented the tubes to the subjects in blocks of five trials per condition, in the following conditions: *banana only*, *one paper*, *two papers*, *rearrange*, and *in/out*. On the first and second days of testing, each subject was presented with five trials of each of the first three conditions: *banana only*, *one paper*, *two papers*. A subject had to achieve 80% success in two consecutive presentations of the same condition, which occurred on different days, to pass to the next condition. In other words, a subject was presented with five trials of *banana only*, five trials of *one paper*, five trials of *two papers* on the first day (even if she failed to pass 80% correct on any condition), and was again presented with five trials in those same conditions on the second day. If she made two errors or fewer between the ten trials of *a single condition*, for example *banana only*, then she passed that condition and on the third

day of testing would begin a session with trials from the next condition, for example, *one paper*, until she achieved 80% success in that condition between two days of testing.

Data collection took place in July and August 2009.

1. *Banana only*

In the first condition, E1 set the tubes on the tray in the predetermined order, picked up the indicated tube to bait, placed one slice of banana into it and set it down on the tray, then presented all five tubes to the subject by sliding the tray up to the cage mesh; this was repeated for five trials (once for each tube and position). The subject watched the entire baiting process, and could see the banana at the time of choice.

2. *One paper*

For five trials in the *one paper* condition, E1 handled each tube, moving from left to right across the tray. For each tube, E1 first showed the subject that it was empty, and then stuffed a small wad of paper in the front end; E1 baited the banana in the pre-determined tube when she came to it, and then stuffed that tube with paper. Because E1 always moved left to right, sometimes the chimpanzee had to wait longer after baiting before making a choice, because E1 was handling and stuffing paper in the other tubes. During these trials, the chimpanzee could not see the banana at the time of choice, and had to remember which tube it was in.

3. *Two papers*

In the third block of trials, E1 stuffed paper into both ends of each tube, in the same manner as before, which took a few seconds extra per tube, overall increasing the length of time that a subject had to remember which tube contained the bait. E1 used two papers to familiarize the chimpanzees with having both ends of the tube blocked: for the planned outdoor competition a paper in each end of the tube would prevent either competitor from “peeking” into the tubes while searching for the reward.

4. *Rearrange*

E1 noticed that some subjects would occasionally poke a finger through the mesh at the position of the baited tube before baiting was completed and hold it there until E1 presented the tray for their choice. To increase the difficulty of the task, E1 rearranged the tubes on the tray after baiting to eliminate any positional cueing. After baiting, E1 would rearrange the tubes to the order of the next trial. For example, E1 would bait in this arrangement: 23145, then shuffle to this arrangement: 41325, then let the subject make a

choice. It was important that the subjects learn to distinguish the tubes by their physical properties (colour, pattern), for the planned protocol for outdoor competition, in which the tubes would be thrown from the tower; chimpanzees would only know which tube was baited, but not where it was located in their enclosure. Rearranging the tubes in full view of the chimpanzees allowed subjects to visually track the movement of the baited tube.

5. *In/out*

As the chimpanzees progressed, E1 attempted to engage their memory further: E1 baited the tubes inside as before, then moved the tray outside; the subject was released into the outdoor enclosure and encouraged to make a choice at the mesh of their outdoor enclosure. For these trials, the subject could not visually track the tubes as the tray was moved. Despite the tubes being visually distinctive, this was very challenging for all subjects, because the apparatus moved and the chimpanzees had to move locations before making a choice. For these trials, the tubes were not rearranged, but since the chimpanzees experienced several trials in that condition before moving to these *in/out* trials, this may have been an illogical progression; subjects may have suspected that I had rearranged or otherwise moved the reward while they were not looking and were largely unsuccessful in this condition.

Since the chimpanzees would not be choosing at the mesh during the competition anyway, E1 moved past the *in/out* trials to let subjects choose among the tubes in their enclosure. To minimize moving in and outdoors, E1 baited the tubes at the outdoor mesh while the subject watched as in the *two paper* condition, and then E1 immediately climbed the stairs to the Viewing Tower directly above the baiting tray, and tossed the tubes into the enclosure.

III. Results

Data are presented for the following conditions: *banana only*, *one paper*, *two papers*, *rearrange*. The results from the *in/out* trials indicated that subjects misunderstood the task, and the protocol was changed shortly after testing in that condition.

A. Individual Results on Tube Training

As the difficulty of the task increased, the chimpanzees' accuracy decreased. Each subject had a different number of total trials because some progressed more quickly than others and therefore did not have to repeat many trials in each condition, and because some testing sessions ended early when a subject stopped participating. Since a subject only needed

80% correct in a condition on *two consecutive sessions* before moving on, percentage scores for total trials in a particular condition are likely to be less than 80%. Certain individuals received more trials in a given condition after they had passed criterion if several days between sessions had passed, or if they were experiencing great difficulty in the new condition, to maintain motivation for the task. Barbie and Julianne were allowed to attempt the *rearrange* condition after five and three sessions of the previous *two papers* condition, respectively, because of testing time constraints.

1. Missy

Missy progressed very quickly, making no errors in the *banana only* condition, making only one mistake in the *one paper* condition in the first ten trials of that type, and achieving 80% success on the *two paper* condition in the first ten trials. Missy experienced difficulty in the *rearrange* condition, so to attempt to make the task more comprehensible, E1 gave her a set of five trials in which E1 rearranged the tubes without the paper stuffing so that Missy could see the banana move with the tubes, and learn the new demand of the task: remembering which tube had the banana, without positional cues. After five familiarization trials, she achieved 90% correct on the next ten *rearrange* trials.

TABLE 3: Missy's total trials in each condition of tube training

Condition	Raw	Total	Percent	Sessions to Criterion
Banana	10	10	100	2
One Paper	9	10	90	2
Two Papers	13	15	86.7	2
Rearrange	13	18	72	3

2. Tara

Tara made many mistakes on her first day of testing, only getting 47% correct overall. After that, she made progress to complete the *one* and *two paper* conditions quickly. Tara stopped participating in her first session including *rearrange* trials, and was not tested again; her 100% success rate does not reflect the total number of trials planned (minimum 10) for the *rearrange* condition.

TABLE 4: Tara's total trials in each condition of tube training

Condition	Raw	Total	Percent	Sessions to Criterion
Banana	13	15	86.7	3
One Paper	17	24	70.8	5
Two Papers	14	19	73.7	3
Rearrange	4	4	100	NA

3. Reinette

Reinette made very few mistakes overall, and mostly in the *rearrange* condition. On two testing days, Reinette ended the session early by refusing to participate.

TABLE 5: Reinette's total trials in each condition of tube training

Condition	Raw	Total	Percent	Sessions to Criterion
Banana	9	10	90	2
One Paper	9	10	90	2
Two Papers	17	20	85	2
Rearrange	8	13	61.5	NA

4. Katie

Katie made frequent errors in the *one-* and *two paper* conditions, delaying her progress to the *rearrange* condition, which also proved quite difficult for her.

TABLE 6: Katie's total trials in each condition of tube training

Condition	Raw	Total	Percent	Sessions to Criterion
Banana	9	10	90	2
One Paper	18	25	72	5
Two Papers	24	33	72.7	4
Rearrange	16	24	66.7	4

5. Tai

To ensure Tai was comfortable being locked inside, she was usually accompanied by one of her daughters, Julianne or Daisy, who did not pay attention or interfere with Tai's training. Tai mostly made mistakes in the *rearrange* condition, and even after some trials in which E1 rearranged the tubes without paper (as done with Missy), she still made several mistakes.

TABLE 7: Tai's total trials in each condition of tube training

Condition	Raw	Total	Percent	Sessions to Criterion
Banana	16	20	80	2
One Paper	12	15	80	2
Two Papers	27	38	71	2
Rearrange	17	36	47.2	NA

6. *Barbie*

Barbie had the most difficulty with the *two papers* and *rearrange* conditions. As with Missy and Tai, Barbie received five additional trials in which E1 rearranged the tubes without the paper stuffing.

TABLE 8: Barbie's total trials in each condition of tube training

Condition	Raw	Total	Percent	Sessions to Criterion
Banana	10	10	100	2
One Paper	8	10	80	2
Two Papers	12	25	48	NA
Rearrange	22	40	55	8

7. *Julianne*

Julianne quickly passed the *banana only* and *one paper* conditions; she only had three sessions indoors before she moved to choosing outside. Since E1 started testing with Julianne later than with the other chimpanzees at FS2, it was already apparent that the *in/out* trials were unsuccessful. Rather than spend time doing *in/out* trials with Julianne, she began testing outside at the same time as the other two chimpanzees in her enclosure, Tai and Barbie, with the tubes dropped from the tower.

TABLE 9: Julianne's total trials in each condition of tube training

Condition	Raw	Total	Percent	Sessions to Criterion
Banana	10	10	100	2
One Paper	9	10	90	2
Two Papers	12	15	80	NA
Rearrange	6	8	75	NA

B. Pooled data

Graph 1 depicts data from FS1: each subject's average percent successful performance (of all trials) in the four conditions *banana only*, *one paper*, *two papers*, and *rearrange*. The general trend is that performance decreases as the difficulty of the task increases. Recall that Tara only completed four *rearrange* trials, so her 100% performance does not reflect the criterion of completing a minimum of ten trials per condition.

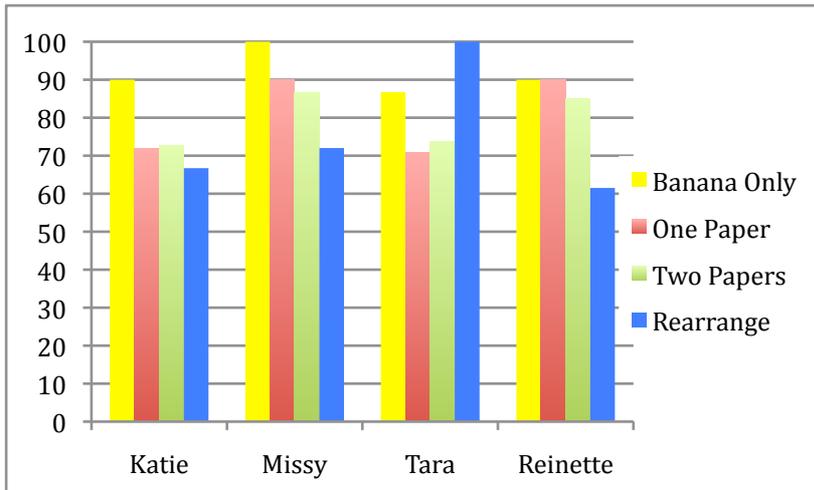


FIGURE 2: Pooled data from FS1, average percent success per individual on each condition

Graph 2 depicts the combined average percent success of the four subjects in FS1 on each condition. Again, the level of success decreases as the demands of the task increase.

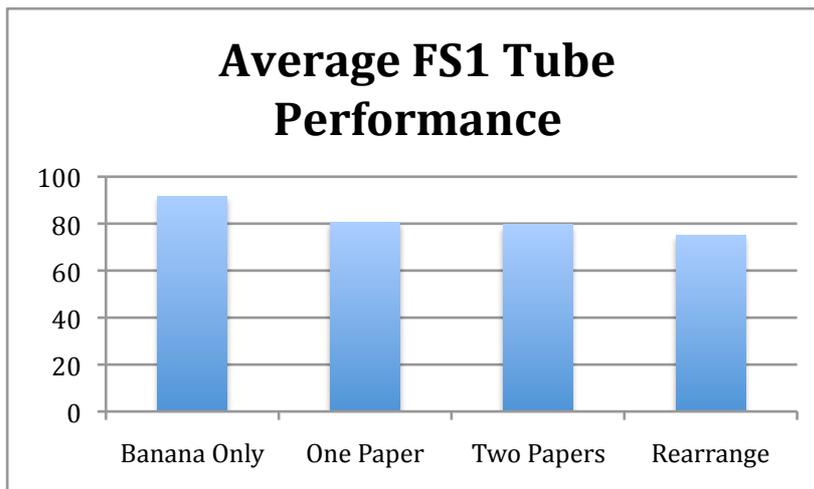


FIGURE 3: Pooled data from FS1, combined average percent success per condition

Graph 3 depicts data from FS2: each subject's average performance in all trials in the four conditions *banana only*, *one paper*, *two papers*, and *rearrange*. As with the chimpanzees from FS1, the trend in the data from FS2 is that performance decreases as the difficulty of the task increases.

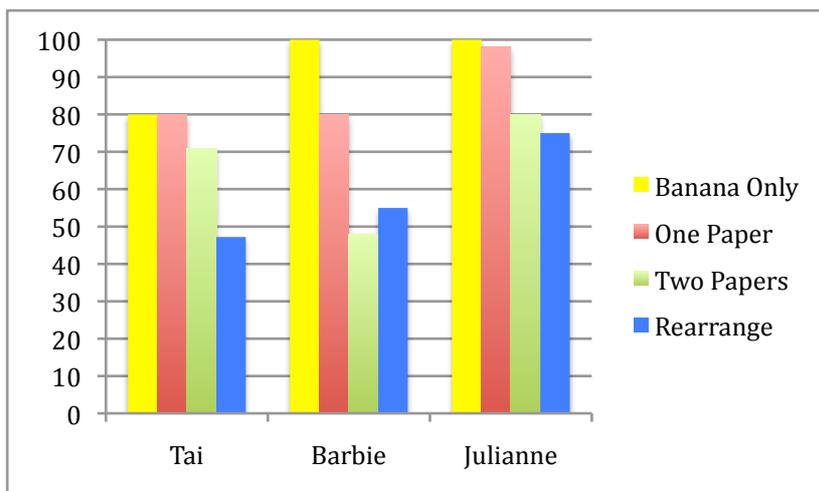


FIGURE 4: Pooled data from FS3, average percent success per individual on each condition

Graph 4 depicts the averages of the three subjects from FS2 on each condition.

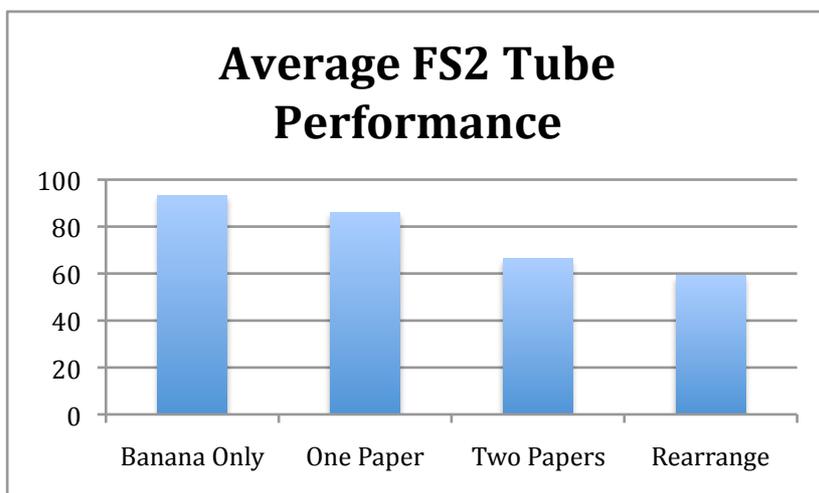


FIGURE 5: Pooled data from FS2, combined average percent success per condition

C. Dropping Tubes into the Enclosure

We attempted a few trials in which the tubes were baited at the mesh of the outdoor enclosure while the subject watched, and then the tubes were dropped from the Viewing Tower into the enclosure for the subject’s choice. The results of these trials are not included in the results in the above sections, because they are inconsistent with the subjects’ successful performance on the training. Based on the chimpanzees’ ability to pass 80% correct tube choices across increasingly difficult conditions, we were confident that the subjects understood that each tube was equally associated with a food reward, and that it was essential

to pay attention during baiting in order to make a correct choice. Though the subjects experienced difficulty moving from inside to outside to make a choice in the *in/out* condition, we expected the chimpanzees to transfer their knowledge of the equal likelihood of bait in each tube to the next step of the training: when we dropped the tubes into the enclosure, we expected the subjects to immediately pick up the baited tube and ignore the empty ones.

For these trials, E1 baited the tubes at the outdoor mesh in front of the subject, while all the other chimpanzees in the group were locked inside. Unlike before, E1 baited the same tube five times in a row to emphasize the importance of the particular tube on that occasion. Then E1 baited the same tube with a half banana—a larger amount than a single slice—and carried all five tubes up to the Viewing Tower directly above where the tubes had been baited, and dropped them into the enclosure. We expected the subjects to go straight towards the baited tube and ignore the empty ones. However, many subjects picked up all the tubes in no particular order, and carried them across the enclosure and opened all of them at the same time, rather than opening each one as it was encountered.

It made no sense that an informed subject would not travel directly to the bait but would search in a seemingly random fashion, even picking up tubes after the baited tube had been found. This “hoarding” behaviour, though unexpected, has several possible explanations. First of all, the chimpanzees had never actually handled the tubes and may have been curious to touch all of them. To reduce the hoarding issue, we tried throwing tubes out in pairs, rather than all five in one trial. We expected that a choice between two tubes should be easier, but still the chimpanzees did not consistently pick up the baited tube first. Another possible reason for their behaviour is that the chimpanzees are accustomed to receiving their afternoon enrichment and other food items throughout the day from the Viewing Tower, so they may have associated the tubes with enrichment rather than research, and expected food to be in all tubes, though that was never the case. Thirdly, there was no significant cost in time, energy, or competitive advantage to pick up each tube, irrespective of its contents (or lack thereof). To increase the cost of picking up all tubes, or at least *not* picking up the baited tube first, we released another chimpanzee from the indoor cages immediately after baiting the tubes at the mesh for the subject, and before dropping the tubes from the tower. For this purpose, we chose a chimpanzee that would not be participating in the informed forager competition, to prevent any learning of the situation. Because the chimpanzees were generally interested in handling the tubes, we expected that another chimpanzee, ignorant to

the bait, would still pick up tubes in a random search, and that this behaviour would motivate the informed subject to narrow her search by prioritizing the tube with the hidden banana. Unfortunately the subjects again did not behave as expected and on several occasions lost the bait to their uninformed mock competitor.

IV. Short Discussion

While all subjects were successful in learning the demands of the tube training in a controlled indoor environment, and were able to pass the 80% correct criterion on each increasingly difficult training condition, they were not able to apply the rules of the training (only one tube baited, a different tube on each trial) to a less controlled outdoor situation. The biggest challenge to the outdoor training was that there was no cost to picking up all five tubes, whereas indoors the subjects were only allowed one choice on each trial. With the availability of five choices, the chimpanzees could not inhibit themselves from picking up all of the tubes. Because of the difficulty in overcoming this problem, we needed to increase the cost of searching so that the subject could more clearly demonstrate that she knew where the food was hidden.

V. Bucket Training Methods

A. Subjects

Most of the same subjects that participated in tube training also participated in bucket training: Katie and Missy from FS1, and Daisy and Julianne from FS2. Barbie and Tai (FS2) did not participate in bucket training: Barbie had participated a lot in trials in which tubes were thrown from the tower, was unsuccessful in finding the bait even with a mock competitor to motivate her, and would unlikely fare better in an actual informed forager competition. Tai chose not to participate, even in the presence of her daughters in the enclosure to maintain her comfort level. Daisy (FS2) joined bucket training since she was comfortable being tested outdoors whereas she had not participated indoors. Since we switched to training the chimpanzees to learn a spatial cue, we did not deem it necessary for Daisy to have experienced the various manipulations that the others had during tube training.

B. Setting

The bucket training initially occurred outdoors at the enclosure mesh with one or two subjects at a time, while the other chimpanzees in the group were locked inside. Baiting

occurred as in the *one paper* condition in tube training, using the wire mesh cart and stuffing paper into the front of each tube. Then, the baited tube was placed into its colour-matched bucket, and the chimpanzee subject was allowed to search. As bucket training progressed, we baited the tubes indoors (in the Cognition Room at FS1 and in the Bedroom area at FS2), and then the tubes were carried outside, and each placed into its corresponding bucket, before releasing the subject outside to search.

C. Behavioural recording

All training sessions were video recorded using a Sony DCR-HC52 camera on a tripod. Subjects' bucket choices were marked on a notepad during the session, and verified on the videotapes afterward.

D. Apparatus

To combat the problem of subjects picking up all five tubes, and to attempt to simplify the task, we set up five white plastic buckets, the bottom end attached with zip-ties to the outside mesh of the outdoor enclosure, so that each bucket was placed horizontally against the mesh. There was a 2 ¼" inch diameter hole cut in the bottom of each bucket, so that a tube (two-inch diameter) could be placed into the bucket from the top end, and a chimpanzee subject could choose a tube by pulling it through the hole in the bucket. Since the chimpanzees were already trained to recognize the five coloured tubes, each bucket would serve as a fixed location for the colour-matching tube. Above the hole, in the centre of the bottom of the bucket, was a painted circle of two-inch diameter corresponding to one of the five colours of the tubes: red, yellow, green, blue, and purple. In both enclosures, the buckets were equally spaced along two walls of the outdoor enclosure so that they were visible for video recording from the Viewing Tower; there were two buckets on one wall and three buckets on the other.

E. Experimental Design

Initially, subjects were trained to associate each tube with its corresponding bucket at its fixed location. This training took place outside along the perimeter mesh of the enclosure; the carry cart with the tubes was set equally spaced between two buckets, for example red and yellow, and only the red and yellow tubes were placed on the cart. The tubes were alternately baited in full view of the subject and placed into their corresponding bucket. To test whether subjects were familiar with matching tubes and buckets, E1 then baited the tubes inside (Cognition Room for FS1 and Bedroom area for FS2) as was done in the *one paper*

condition of tube training, then as the subject waited inside, E1 carried the tubes outside and placed each tube in its corresponding bucket.

F. Procedure

To train the chimpanzees to associate each tube with its specific bucket, we first set up the baiting tray at the enclosure mesh, between two buckets. E1 baited one tube with a banana slice and piece of paper, then deposited the tube into its bucket, and let the subject pull the tube through the hole in the bucket. After five trials with the same tube and bucket, E1 switched to the adjacent tube and bucket for five trials. Then, E1 placed both tubes on the baiting tray, and baited only one; E1 and a second experimenter E2 each took one tube, walked to the corresponding bucket, and deposited the tube. If the chimpanzee remembered which tube had the bait, she could watch which experimenter picked it up, and track the physical displacement of the tube into the bucket (no more than three meters distance, known as *close* trials). This process was repeated for each adjacent tube/bucket pair.

The next step of bucket training was to bait the tubes in a different location than directly next to the matching bucket (*far* trials, tubes were baited approximately 30 meters from their matching buckets); for this procedure, the baiting tray was set up in the corner of the enclosure beneath the Viewing tower, opposite both walls to which buckets were attached. Again, E1 baited one of two tubes on the tray, and E1 and E2 each carried a tube to its bucket. Because both experimenters had to travel some distance, often behind a building or some visual barrier, it was key that the subject could remember which tube had the banana, because she could not visually track the movement of the baited tube at all times. Furthermore, E1 and E2 occasionally traded tubes while walking behind the building to prevent any association with the experimenter that carried the baited tube on a particular trial.

In the third step of bucket training, we baited one of five tubes indoors as had been done during the *one paper* tube training; then as the subject was locked inside, E1 and E2 walked outside and placed the tubes in their buckets, and then released the subject outside. To demonstrate that the subjects had associated each tube with a specific bucket location, and that they remembered which tube had been baited (for several minutes, while not being able to witness the physical displacement of the tubes), the subjects would have to approach the correct tube and bucket first, before inspecting the others.

Data collection took place during September and October 2009.

VI. Results

All subjects were keen to pull the baited tubes through the holes in their matching buckets. However, when given a choice between two tubes, with only one baited, success was rather low. When two tubes were baited at the outdoor mesh and carried by E1 and E2 to their respective buckets, from either a short or far distance, subjects did not always choose the baited bucket first. In close and far trials, Daisy picked the correct bucket on 62.5% and 60% of trials, respectively. Julianne picked the correct bucket on 0% of close trials and 71.4% of far trials. Katie chose the correct bucket on 100% of close trials, and 30% of far trials. Missy chose correctly on 71.4% of close trials, and 50% of far trials.

As training progressed in the *far* trials, some subjects would begin to walk to the correct bucket and wait for the experimenter to arrive, which was a good indication that they understood the association between the tubes and buckets. When E1 baited one tube inside and hid only that tube in its bucket, without placing the other empty tubes in their buckets, the chimpanzees walked directly to the correct bucket when released outside.

During the third step of bucket training, when E1 placed the other empty tubes in their buckets as well as the baited one in its correct place, the subjects checked all five buckets always in the same order, did not go directly to the baited tube, and continued to check buckets after finding the baited tube. There was no major cost for searching in more than one place other than time and distance travelled, and in captivity these can hardly be considered costs, since the chimpanzees were well fed and in a small, protected area.

VII. Short Discussion

When the chimpanzees were trained to identify the various tubes used in the previous experiment, they did not immediately pick up the correct one when allowed to handle all five, nor did they pick up only the correct tube. The purpose of training the chimpanzees to search for food in a bucket at a fixed location was to compel them to choose the correct location first in the absence of a competitor, and to stop searching after finding the bait. Like tube training, bucket training was only partially successful when the number of choices was limited to two. But with five choices available, the chimpanzees could not inhibit themselves from looking in each bucket.

The idea of tubes and buckets as hiding locations seemed straightforward and controllable for a research study, but the cost of searching all locations was not high enough,

nor were subjects prevented from doing so. In terms of studying knowledge and ignorance in the informed forager competition, we wanted to be certain that the subject understood where the food was hidden, and would go directly to it; any behaviour such as delaying walking to the reward, or searching other locations first, could be interpreted as withholding or misleading a competitive foraging partner. But since the chimpanzees exhibited these behaviours in the absence of a partner, it would be difficult to compare baseline behaviours with competition behaviours.

However, with such limited success identifying the correct bucket when only two of five choices were available, we were sceptical that this method would allow us to test the knowledge of the informed competitor. Following these two failed attempts to train the chimpanzees to associate tubes and buckets with a hidden food reward, we again changed our protocol for the informed forager paradigm.

VIII. Conclusion

Originally, Menzel (1974) carried out his informed forager experiments by hiding food in the chimpanzees' enclosure without any advertising, i.e., the food was not hidden in a special container used only in the context of the study. Naïve subjects only knew to search for food when reading the behaviour of their knowledgeable groupmate. In the current study, the inherent novelty of tubes or buckets in or around the edge of the enclosure motivated exploration even in the absence of food, possibly because previous studies with these subjects involved exchanging tubes for a reward, and so the chimpanzees may have associated all tubes with a reward for every trial (Brosnan & de Waal, 2005; Brosnan et al., 2005; Bonnie et al., 2007; Horner et al., 2010), though that was not the case in the current study. Other studies that have used designated containers (Coussi-Korbel, 1994; Held et al., 2000, 2002, 2005, 2010; Bugnyar & Kotrschal, 2004) have the benefit that all subjects were aware of being in a testing situation, but with the limitation that the ignorant subjects could explore all containers and find the food using that strategy but not necessarily relying on any information to be gained from a knowledgeable partner.

I changed the protocol in order to make the informed forager competition as clear as possible for the subjects: I eliminated the tubes and buckets to reduce memory constraints, and instead E1 entered the enclosure and hid a banana in a place naturally afforded by the features of the enclosure and the objects in it (for example, in a tire, in a hole, under a barrel,

etc.) while a chimpanzee watched through a small Lexan window, following the methods of Menzel (1974) and Hirata & Matsuzawa (2001). This method involves no training; the subject can see exactly where the food is hidden, and there is no special apparatus such as a tube or bucket.

Appendix to Chapter 4: Figures from previous informed forager analyses

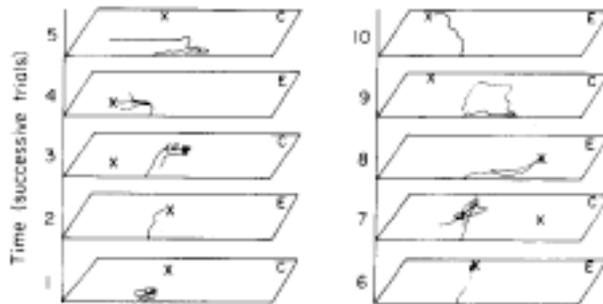


FIG. 17. Maps showing the travel routes taken by the group as a whole on each of 10 successive trials on Bandit's Day 2 performance as leader. E = experimental condition, with Bandit as leader; C = control condition, with no one shown the location of the hidden food. All other chimps tested as leader performed as well as this on their first tests. [Based on Menzel (1971a).]

FIGURE 4.1: Maps taken with permission from Menzel (1974) showing a chimpanzee group's travel routes in their enclosure; E indicates an experimental condition in which a chimpanzee, Bandit, was shown a hidden food item, and C indicates a control condition in which no chimpanzee was shown a hidden food.

FIGURE 4.2 (Next page): Table taken with permission from Ducoing & Thierry (2003) showing the duration of the ignorant subject monitoring the informed subject.

Table 1

Duration of Monitoring of the Informed Subject by the Uninformed Subject: Comparison of Lower and Higher Ranking Subjects

% of time spent	Weakly asymmetrical dyads (<i>N</i> = 10 trials)						Strongly asymmetrical dyads (<i>N</i> = 15 trials)					
	First dyad			Second dyad			First dyad			Second dyad		
	Lower ranking (Vac)	Higher ranking (Vic)	<i>p</i>	Lower ranking (Vor)	Higher ranking (Bul)	<i>p</i>	Lower ranking (Vic)	Higher ranking (Bul)	<i>p</i>	Lower ranking (Vac)	Higher ranking (Vor)	<i>p</i>
Following	57.1 ± 9.0	56.3 ± 10.9		21.1 ± 9.6	50.4 ± 8.6		27.0 ± 7.2	17.3 ± 5.4		8.1 ± 4.9	13.0 ± 3.6	
Keeping tabs	29.0 ± 8.0	43.1 ± 10.8		71.6 ± 10.3	36.8 ± 8.5		59.7 ± 7.2	44.1 ± 5.3		58.7 ± 8.8	38.7 ± 7.4	
Total monitoring	86.1 ± 6.7	99.4 ± 7.6	.028	92.2 ± 9.0	87.2 ± 6.1	.285	86.7 ± 5.9	61.4 ± 4.5	.031	66.8 ± 6.7	51.7 ± 4.7	.198

Note. The duration of monitoring is calculated as the sum of the duration of following and keeping tabs. Table shows means plus or minus standard errors of the means. Statistics use the Wilcoxon signed-ranks test.

Table 4
Development and Function of Rapide's Behavior When Not Going Directly to the Food in the First Experimental Condition

Direction of movement and context	Trial	Subsequent approach the food?	Food obtained?	Function and outcome
Going in the opposite direction from the food				
Boss follows	2	No	No	Avoidance of aversive social control
Boss follows	3	Yes ^a	Yes	Attracting Boss's attention elsewhere
Boss follows	13	Yes ^a	Yes	Attracting Boss's attention elsewhere
Rapide follows group	21	(Yes) ^b	Yes	Social cohesion
Boss is the first to enter provisioned zone	24	(Yes) ^b	Yes	?
Passing by the food				
Boss follows	4	Yes ^a	Yes	Attracting Boss's attention elsewhere
Boss follows	10	Yes ^a	No	Attracting Boss's attention elsewhere
Withdrawing from the food				
Boss follows	6	(Yes) ^b	No	?
Boss follows	8	No	No	Avoidance of aversive social control
Boss is the first to enter provisioned zone	19	Yes ^a	Yes	Withholding the information
Boss follows	22	Yes ^a	Yes	Withholding the information
Stopping halfway there				
Boss is the first to enter provisioned zone	20	Yes ^a	Yes	Withholding the information

^a Movement patterns that have been classified as the taking of an indirect route to the goal. ^b Absence of a temporal contiguity between Boss's being occupied elsewhere and Rapide's subsequent approach to the goal.

FIGURE 4.3: Table taken with permission from Coussi-Korbel (1994) showing the development and function of the informed subordinate Rapide's behaviour (Boss is the ignorant dominant).

FIGURE 4.4 (Next page): Table taken with permission from Hirata & Matsuzawa (2001) showing the progress of the interaction between two chimpanzees, Chloe and Pendesa, that were alternately informed or ignorant of the hidden food's location. Several actions were recorded for both subjects.

Table 1 Progress of pair A. The 2nd and 3rd rows from top show the experimental condition, i.e., which role each individual took. The 4th row shows the name of individual who first went out to the compound when the door opened. The 6–17th rows provide information about Pendesa’s behavior. Asterisks in the 6–11th rows indicate that a particular behavior

was observed inside the waiting room or in the outdoor compound before one of the subjects obtained the hidden banana. Numbers in the 12–16th rows represent the number of times each behavior was counted. The last two rows from top provide information about Chloe’s behaviors (Ch Chloe, Pe Pendesa, DTOR degree of taking the optimal route)

Day	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	
Witness	Chloe								Pendesa			Chloe			Pendesa			Chloe										Neither							
Witness-of-witness	Pendesa								Chloe			Pendesa			Chloe			Pendesa																	
Who came out first?	Pe	Pt	Ch	Pe	Pe	Pe	Pe	Pe	Pe	Pe	Pe	Pe	Pe	Pe	Pe	Pe	Ch	Pe	Pe	Pe	Pe	Pe	Pe	Pe	Pe	Pe	Pe	Pe	Pe	Pe	Pe	Pe	Pe	Pe	
Who got the banana?	Ch	Pt	Ch	Ch	Ch	Ch	Pe	Ch	Pe	Pe	Pe	Ch	Pe	Ch	Pe	Pe	Pe	Pe	Pe	Ch	Ch	Ch	Ch	Ch	Ch	Ch	Pe	Ch	Pe	Ch	Pe	Ch	Pe	Pe	
Pendesa’s behaviors toward Chloe In the compound	Threat in the room																																		
	Seek banana				*		*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
	Threat											*	*	*	*	*			*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	
	Pursue																			*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	
	Adjust direction																			*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	
	Wait																											*	*	*	*	*	*	*	
	Frequency of looking	1	1	0	1	1	0	3	0	0	1	3	2	2	4	1	1	2	1	1	2	4	1	2	5	4	3	6	7	5	12	7	2	10	7
	Neglect					1		2							2	1		1	1	1		1			2	1		1				2		2	1
	Neutral	1	1		1			1			1	3	2	2	2		1	1				1	1	1		1	1	4	4	4	5	4	2	5	5
	Pursue																				1	2		1	3	1	1		2	3		1	1		
Adjust direction																				1					1	1	1	1	1	4	1				
DTOR (%)	7	100	21	9	11	8	59	5	100	100	100	4	2	6	24	100	18	24	10	4	23	4	11	19	19	3	33	46	14	46	35	17	2	30	
Chloe	DTOR (%)	100	100	100	100	100	41	100	5	12	17	100	100	100	63	9	9	24	17	100	100	100	100	58	38	100	73	59	100	72	42	100	6	54	
	Misleading behavior																							*	*	*	*	*	*	*	*	*	*	*	

Appendix to Chapter 5: Control graphs for “Walking Towards the Bait”

I. Pair 1 (Missy and Rita) Control Graphs for “Walking Towards the Bait”

Cross Correlation, Pair 1 *No Knowledge*: When the Subordinate Walks Towards the Bait, Does the Dominant Walk Towards the Bait?

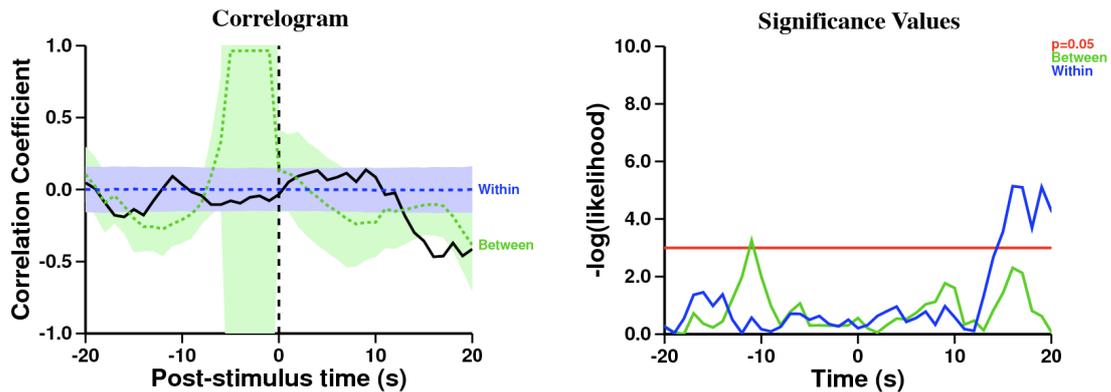


FIGURE 5.1: Referent behaviour: subordinate walking towards the bait. Target behaviour: dominant walking towards the bait. There is no relationship between the two variables until many seconds after the subordinate walks towards the bait, the dominant walks towards the bait significantly less than expected from the within-trial shuffled control (peak at time= +19, $r = -0.4610$, $n = 42$; $-\log(\text{likelihood}) = 5.1118$, $p < 0.05$)

Cross Correlation, Pair 1 *Full Knowledge*: When the Subordinate Walks Towards the Bait, Does the Dominant Walk Towards the Bait?

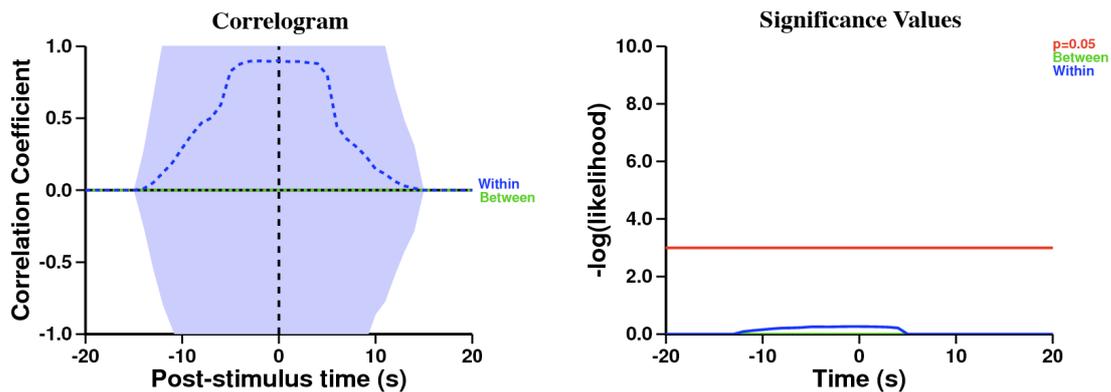


FIGURE 5.2: Referent behaviour: subordinate walking towards the bait. Target behaviour: dominant walking towards the bait. There is no relationship between the two variables, and this is likely to be an effect of small sample size.

II. Pair 2 (Reinette and Georgia) Control Graphs for “Walking Towards the Bait”

Cross Correlation, Pair 2 *No Knowledge*: When the Subordinate Walks Towards the Bait, Does the Dominant Walk Towards the Bait?

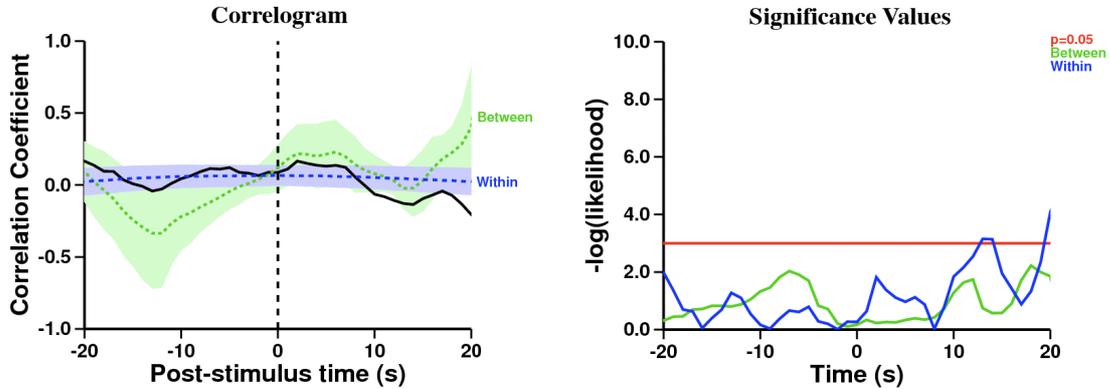


FIGURE 5.3: Referent behaviour: subordinate walking towards the bait. Target behaviour: dominant walking towards the bait. After the subordinate walks towards the bait, the dominant walks towards the bait, and this relationship trends towards being more than expected from the within-trial shuffled control (peak at time= +2, $r = 0.1658$, $n = 185$; $-\log\text{-likelihood} = 1.8168$, *ns*). A few seconds later, the dominant walks towards the bait significantly less than expected from the within-trial shuffled control (peak at time= +20, $r = -0.2060$, $n = 116$; $-\log\text{-likelihood} = 4.0836$, $p < 0.05$).

Cross Correlation, Pair 2 *Full Knowledge*: When the Subordinate Walks Towards the Bait, Does the Dominant Walk Towards the Bait?

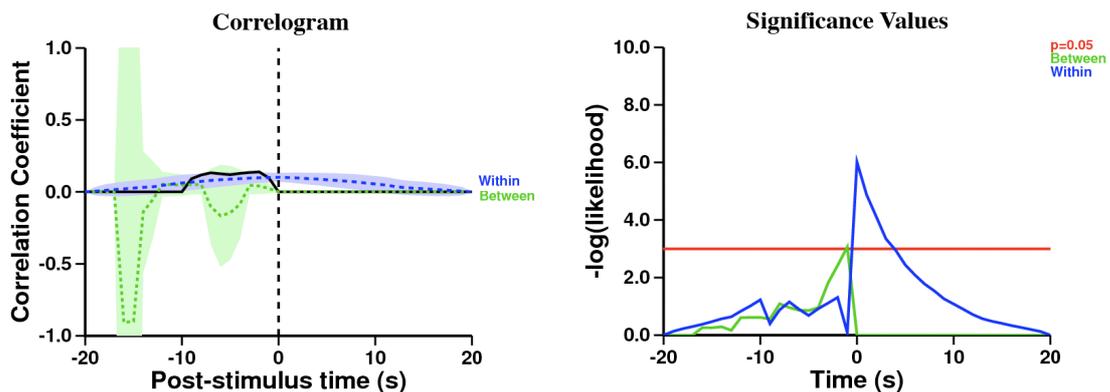


FIGURE 5.4: Referent behaviour: subordinate walking towards the bait. Target behaviour: dominant walking towards the bait. After the subordinate walks towards the bait, the dominant walks towards the bait significantly less than expected from the within-trial shuffled control (peak at time= 0, $r = 0.0000$, $n = 29$; $-\log\text{-likelihood} = 6.0136$, $p < 0.05$), though this is likely an effect of small sample size.

Appendix to Chapter 6: Control graphs for “Gazing Towards the Bait;” Gaze graphs for Phases 1-3

I. Pair 1 (Missy and Rita) Control Graphs for “Gazing Towards the Bait”

II. Pair 1 (Missy and Rita) Graphs from Phases 1-3

A. Static Gaze Following

1. Phase 1
2. Phase 2
3. Phase 3

B. Following Gaze Onset

1. Phase 1
2. Phase 2
3. Phase 3

III. Pair 2 (Reinette and Georgia) Control Graphs for “Gazing Towards the Bait”

IV. Pair 2 (Reinette and Georgia) Graphs from Phases 1-3

A. Static Gaze Following

1. Phase 1
2. Phase 2
3. Phase 3

B. Following Gaze Onset

1. Phase 1
2. Phase 2
3. Phase 3

I. Pair 1 (Missy and Rita) Control Graphs for “Gazing Towards the Bait”

Cross Correlation, Pair 1 *No Knowledge*: When the Subordinate Gazes Towards the Bait, Does the Dominant Gaze Towards Bait?

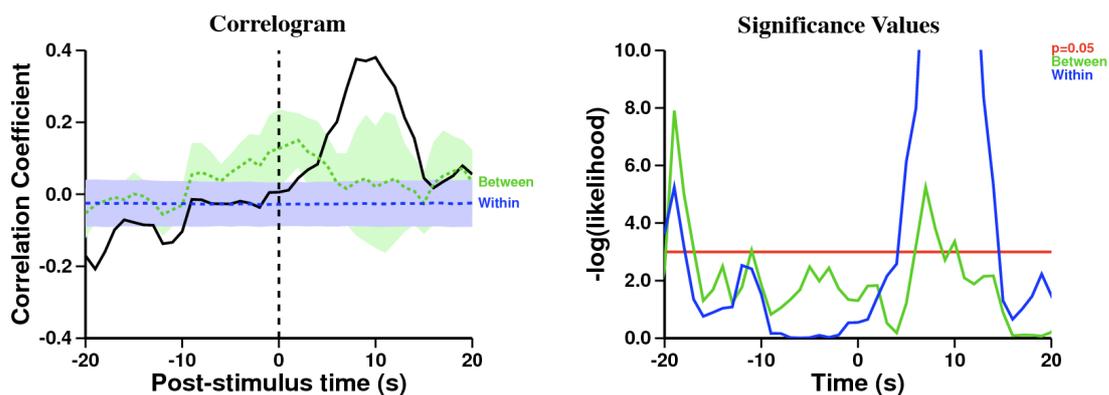


FIGURE 6.1: Referent behaviour: Subordinate gazing towards the bait. Target behaviour: dominant gazing towards the bait. After the subordinate gazes towards the bait, the dominant gazes towards the bait significantly more than expected from the within-trial shuffled control (peak at time= +8, $r = 0.3756$, $n = 235$; $-\log\text{-likelihood} = 21.0918$, $p < 0.05$). Before the subordinate gazes towards the bait, the dominant gazes towards the bait less than expected

from the within-trial shuffled control (peak at time= -19, $r = -0.2078$, $n = 248$; $-\log$ -likelihood= 5.2435, $p < 0.05$).

Cross Correlation, Pair 1 Full Knowledge: When the Subordinate Gazes Towards the Bait, Does the Dominant Gaze Towards the Bait?

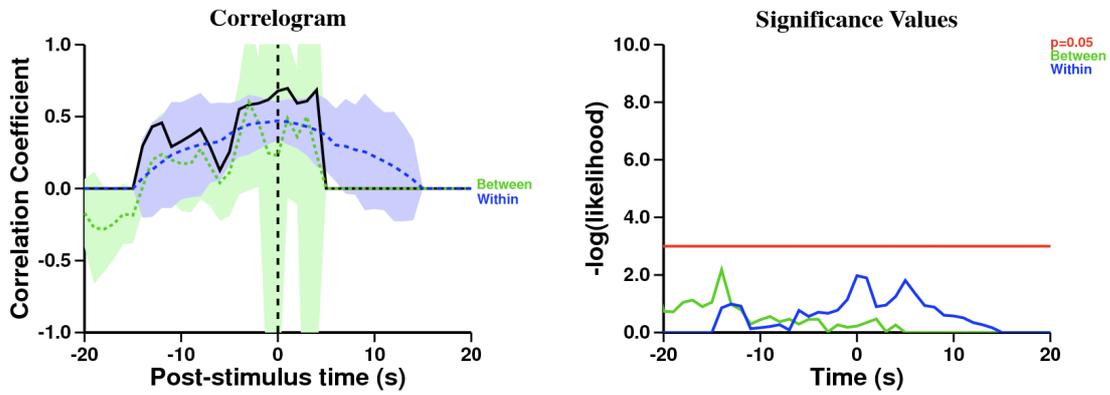


FIGURE 6.2: Referent behaviour: Subordinate gazing towards the bait. Target behaviour: dominant gazing towards the bait. When the subordinate gazes towards the bait, the dominant gazes towards the bait, and this relationship trends towards being more than expected from the within-trial shuffled control (peak at time= 0, $r = 0.6778$, $n = 29$; $-\log$ -likelihood= 1.9742, *ns*).

II. Pair 1 (Missy and Rita) Graphs from Phases 1-3

A. Static Gaze Following

1. Phase 1

Cross Correlation, Pair 1 Phase 1: When the Dominant Looks at the Subordinate, Do They Both Gaze Towards the Same Quadrant?

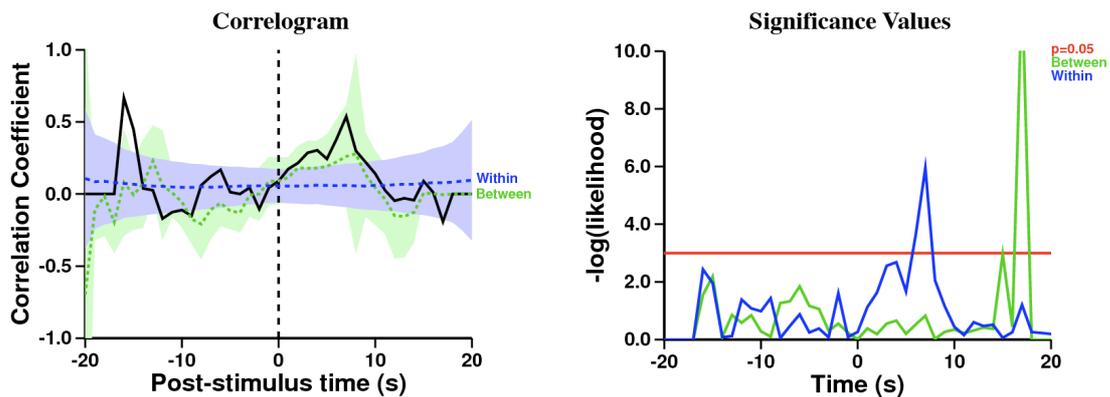


FIGURE 6.3: Referent behaviour: dominant looking at subordinate. Target behaviour: both chimpanzees gazing towards the same quadrant. After the dominant looked at the subordinate, both chimpanzees gazed towards the same quadrant significantly more than expected from the within-trial shuffled control (peak at time= +7, $r = 0.5378$, $n = 55$; $-\log$ -likelihood= 5.9478, $p < 0.05$).

Cross Correlation, Pair 1 Phase 1: When the Subordinate Looks at the Dominant, Do They Both Gaze Towards the Same Quadrant?

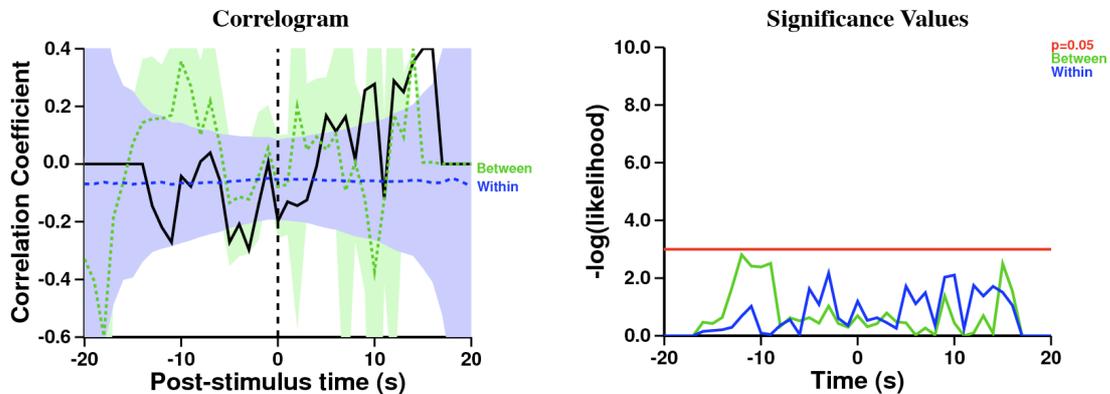


FIGURE 6.4: Referent behaviour: subordinate looking at dominant. Target behaviour: both chimpanzees gazing towards the same quadrant. There is no significant relationship between the variables, but the pattern in the correlogram indicates a positive trend (peak at time= +10, $r = 0.2774$, $n = 18$; $-\log\text{-likelihood} = 2.1034$, *ns*).

2. Phase 2

Cross Correlation, Pair 1 Phase 2: When the Dominant Looks at the Subordinate, Do They Both Gaze Towards the Same Quadrant?

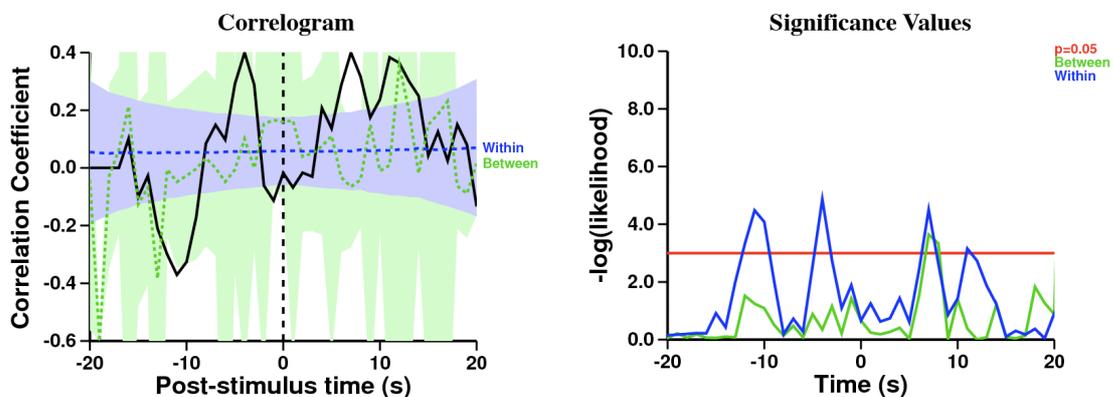


FIGURE 6.5: Referent behaviour: dominant looking at subordinate. Target behaviour: both chimpanzees gazing towards the same quadrant. After the dominant looked at the subordinate, both chimpanzees gazed towards the same quadrant significantly more than expected from the within-trial shuffled control (peak at time= +7, $r = 0.4108$, $n = 76$; $-\log\text{-likelihood} = 4.5044$, $p < 0.05$). Before the dominant looked at the subordinate, both chimpanzees alternated between gazing towards different quadrants (peak at time= -11, $r = -0.3707$, $n = 27$; $-\log\text{-likelihood} = 4.4804$, $p < 0.05$) and towards the same quadrant (peak at time= -4, $r = 0.4075$, $n = 58$; $-\log\text{-likelihood} = 4.8672$, $p < 0.05$).

Cross Correlation, Pair 1 Phase 2: When the Subordinate Looks at the Dominant, Do They Both Gaze Towards the Same Quadrant?

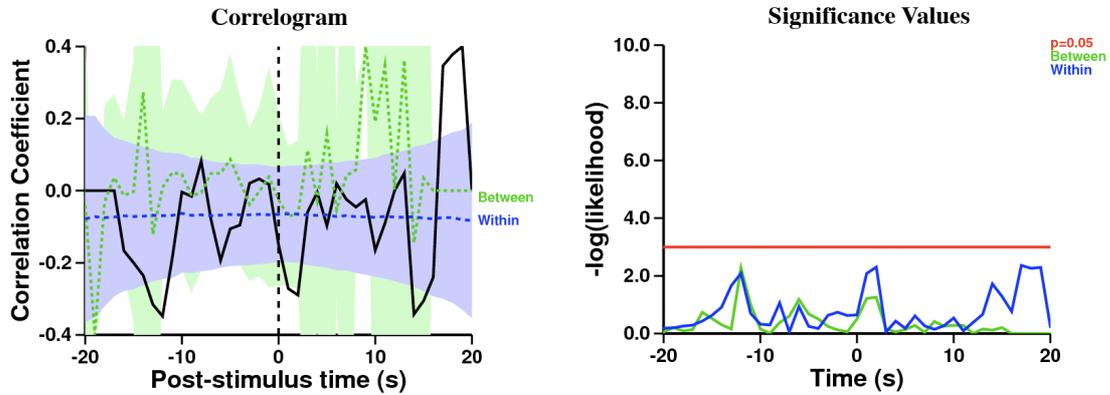


FIGURE 6.6: Referent behaviour: subordinate looking at dominant. Target behaviour: both chimpanzees gazing towards the same quadrant. After the subordinate looked at the dominant, both chimpanzees gazed towards the same quadrant; this relationship trends towards being less than expected from the within-trial shuffled control (peak at time= +2, $r = -0.2898$, $n = 70$; $-\log\text{-likelihood} = 2.3023$, ns).

3. Phase 3

Cross Correlation, Pair 1 Phase 3: When the Dominant Looks at the Subordinate, Do They Both Gaze Towards the Same Quadrant?

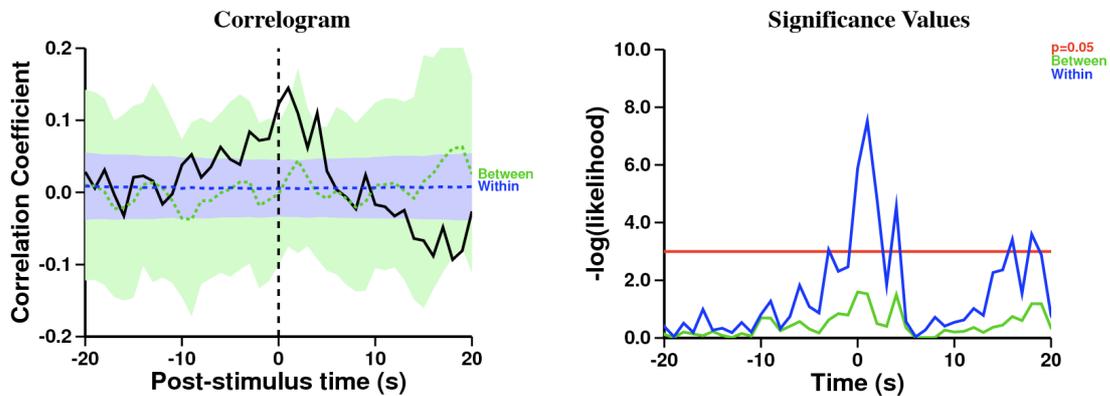


FIGURE 6.7: Referent behaviour: dominant looking at subordinate. Target behaviour: both chimpanzees gazing towards the same quadrant. After the dominant looked at the subordinate, both chimpanzees gazed towards the same quadrant significantly more than expected from the within-trial shuffled control (peak at time= +1, $r = 0.1448$, $n = 700$; $-\log\text{-likelihood} = 7.5194$, $p < 0.05$).

Cross Correlation, Pair 1 Phase 3: When the Subordinate Looks at the Dominant, Do They Both Gaze Towards the Same Quadrant?

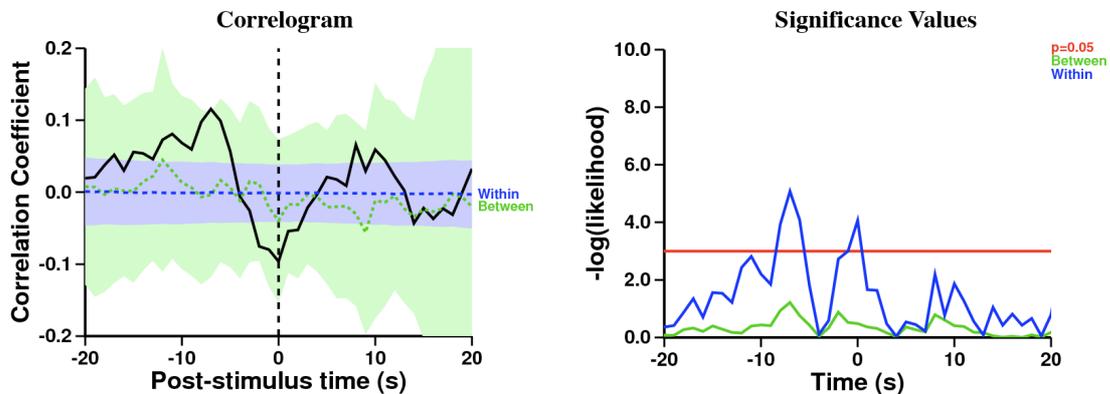


FIGURE 6.8: Referent behaviour: subordinate looking at dominant. Target behaviour: both chimpanzees gazing towards the same quadrant. After the subordinate looked at the dominant, the chimpanzees did not gaze towards the same quadrant (peak at time= 0, $r = -0.0963$, $n = 704$; $-\log\text{-likelihood} = 4.0665$, $p < 0.05$). Before the subordinate looked at the dominant, both gazed towards the same quadrant significantly more than expected from the within-trial shuffled control (peak at time= -7, $r = 0.1156$, $n = 615$; $-\log\text{-likelihood} = 5.0758$, $p < 0.05$).

B. Following Gaze Onset

1. Phase 1

Cross Correlation, Pair 1 Phase 1: When the Subordinate Changes Gaze Direction in View of the Dominant, Do They Both Gaze Towards the Same Quadrant?

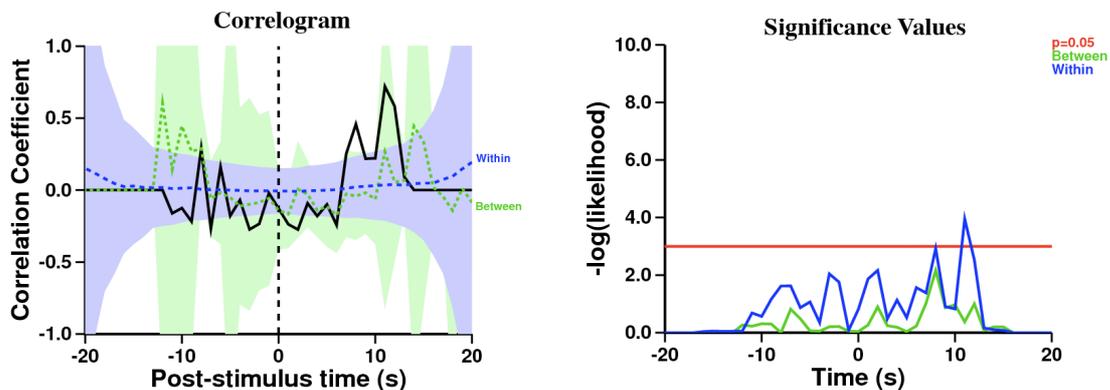


FIGURE 6.9: Referent behaviour: subordinate changes gaze direction in view of the dominant. Target behaviour: both chimpanzees gazing towards the same quadrant. After the subordinate changed her gaze direction, both chimpanzees gazed towards the same quadrant (peak at time= +11, $r = 0.7201$, $n = 13$; $-\log\text{-likelihood} = 3.9546$, $p < 0.05$).

Cross Correlation, Pair 1 Phase 1: When the Dominant Changes Gaze Direction in View of the Subordinate, Do They Both Gaze Towards the Same Quadrant?

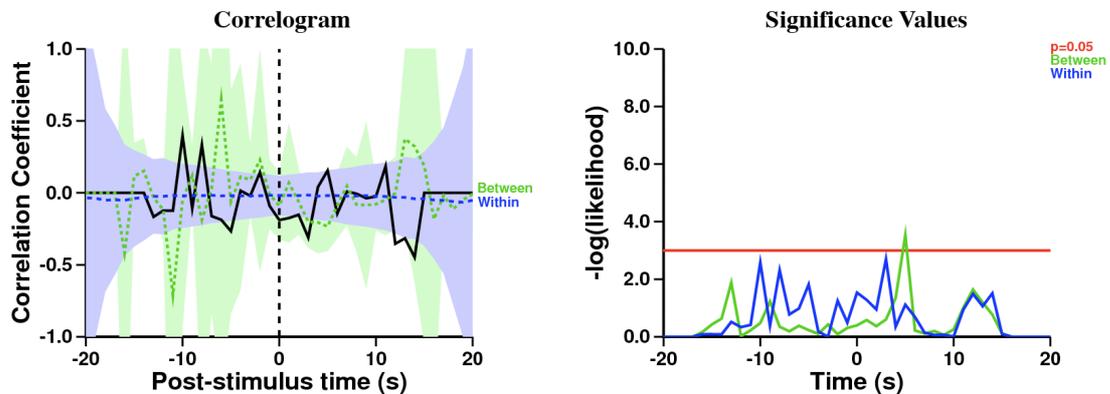


FIGURE 6.10: Referent behaviour: dominant changes gaze direction in view of the subordinate. Target behaviour: both chimpanzees gazing towards the same quadrant. After the dominant changed her gaze direction in view of the subordinate, both chimpanzees gazed towards the same quadrant; this relationship trends towards being less than expected from the within-trial shuffled control (peak at time= +3, $r = -0.3106$, $n = 52$; $-\log\text{-likelihood} = 2.6970$, ns).

2. Phase 2

Cross Correlation, Pair 1 Phase 2: When the Subordinate Changes Gaze Direction in View of the Dominant, Do They Both Gaze Towards the Same Quadrant?

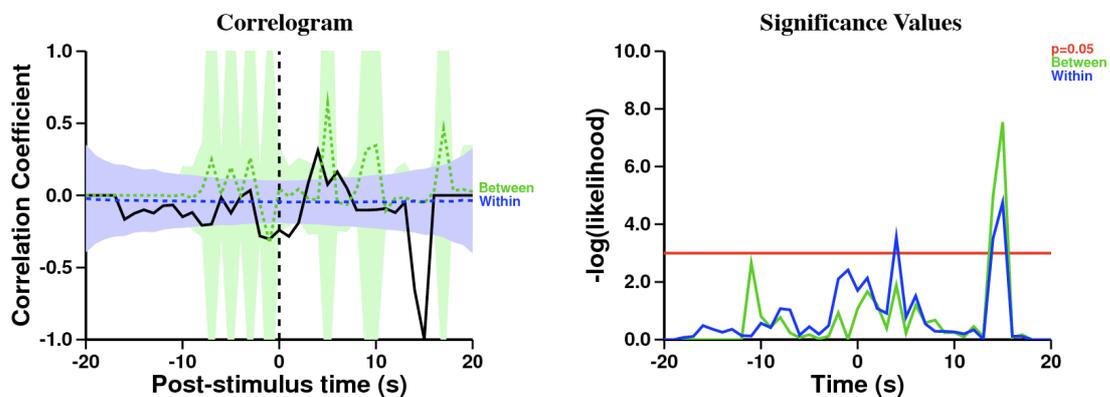


FIGURE 6.11: Referent behaviour: subordinate changes gaze direction in view of the dominant. Target behaviour: both chimpanzees gazing towards the same quadrant. After the subordinate changed her gaze direction, both chimpanzees gazed towards the same quadrant (peak at time= +4, $r = 0.3110$, $n = 31$; $-\log\text{-likelihood} = 3.5485$, $p < 0.05$). Later, the chimpanzees did not gaze towards the same quadrant (peak at time= +15, $r = -1.0000$, $n = 7$; $-\log\text{-likelihood} = 4.7570$, $p < 0.05$).

Cross Correlation, Pair 1 Phase 2: When the Dominant Changes Gaze Direction in View of the Subordinate, Do They Both Gaze Towards the Same Quadrant?

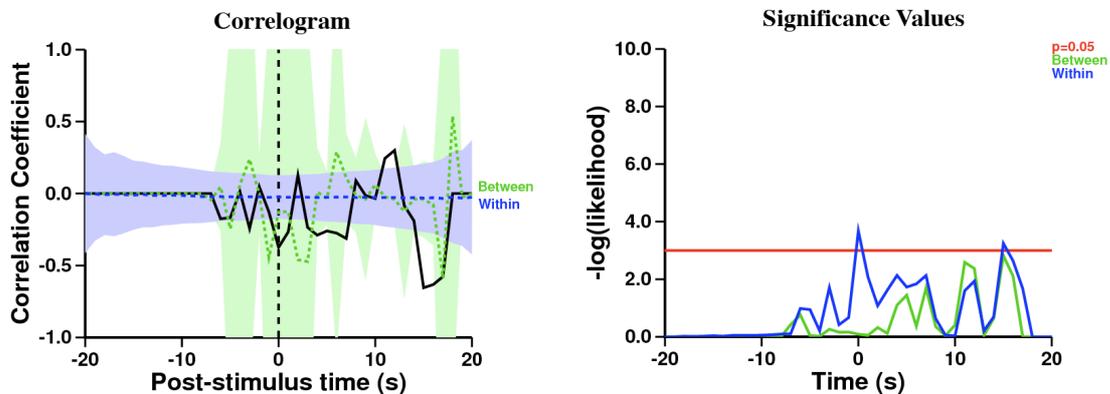


FIGURE 6.12: Referent behaviour: dominant changes gaze direction in view of the subordinate. Target behaviour: both chimpanzees gazing towards the same quadrant. At the moment that the dominant changed her gaze direction in view of the subordinate, the chimpanzees did not gaze together towards the same quadrant (peak at time= 0, $r = -0.3742$, $n = 43$; $-\log\text{-likelihood} = 3.6790$, $p < 0.05$). The relationship alternates and becomes significant at time= +15, when the chimpanzees are gazing towards the same direction significantly less than expected from the within-trial shuffled control (time= +15, -0.6547 , $n = 8$; 3.2432 , $p < 0.05$).

3. Phase 3

Cross Correlation, Pair 1 Phase 3: When the Subordinate Changes Gaze Direction in View of the Dominant, Do They Both Gaze Towards the Same Quadrant?

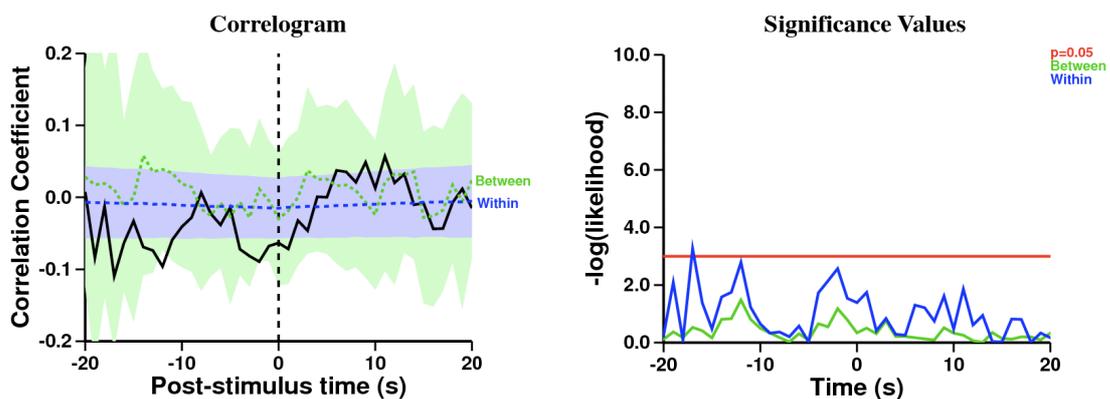


FIGURE 6.13: Referent behaviour: subordinate changes gaze direction in view of the dominant. Target behaviour: both chimpanzees gazing towards the same quadrant. Before the subordinate changed her gaze direction in view of the dominant, both chimpanzees gazed towards the same quadrant; this relationship trends towards being less than expected from the within-trial shuffled control (peak at time= -2, $r = -0.0894$, $n = 576$; $-\log\text{-likelihood} = 2.5695$, ns), and then after the subordinate changed gaze direction, there was no relationship of both chimpanzees gazing towards the same quadrant.

Cross Correlation, Pair 1 Phase 3: When the Dominant Changes Gaze Direction in View of the Subordinate, Do They Both Gaze Towards the Same Quadrant?

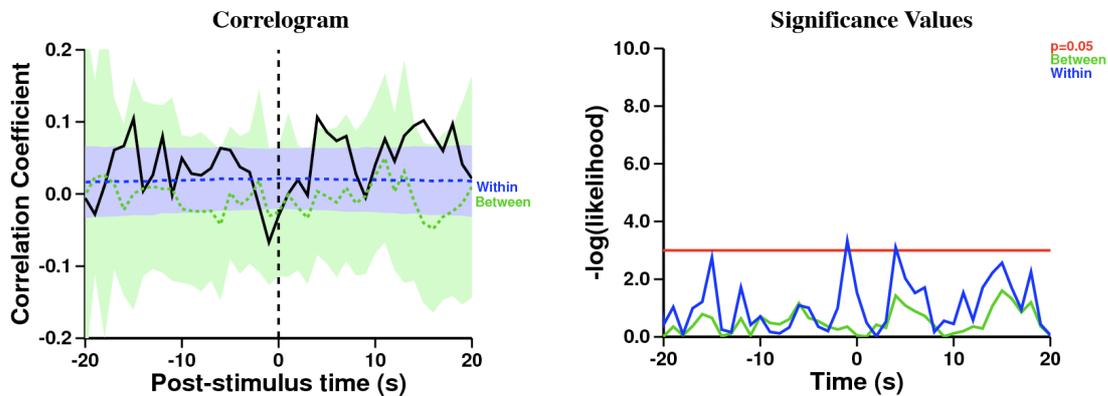


FIGURE 6.14: Referent behaviour: dominant changes gaze direction in view of the subordinate. Target behaviour: both chimpanzees gazing towards the same quadrant. Before the dominant changed her gaze direction in view of the subordinate, the chimpanzees did not gaze towards the same quadrant (peak at time= -1, $r = -0.0671$, $n = 641$; $-\log\text{-likelihood} = 3.3344$, $p < 0.05$). After the dominant changed gaze direction, both chimpanzees gazed towards the same quadrant significantly more than expected from the within-trial shuffled control (peak at time= +4, $r = 0.1067$, $n = 592$; $-\log\text{-likelihood} = 3.1020$, $p < 0.05$).

III. Pair 2 (Reinette and Georgia) Control Graphs for “Gazing Towards the Bait”

Cross Correlation, Pair 2 No Knowledge: When the Subordinate Gazes Towards the Bait, Does the Dominant Gaze Towards the Bait?

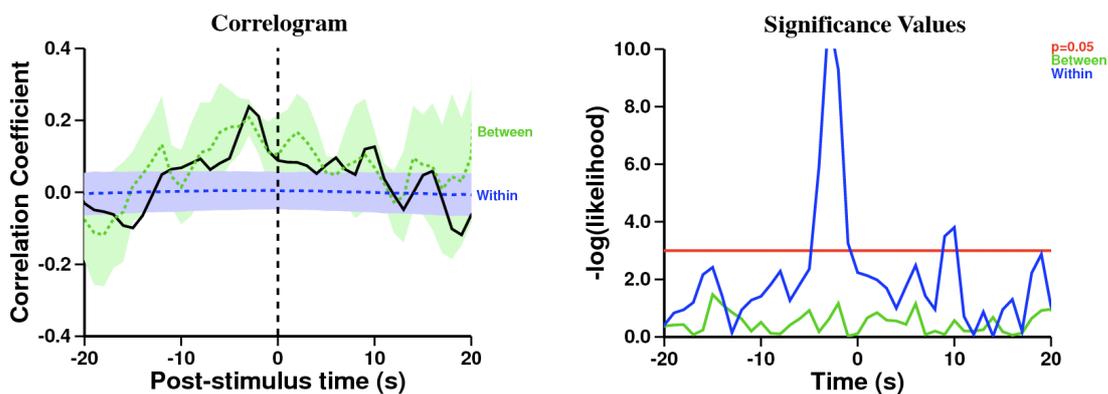


FIGURE 6.15: Referent behaviour: Subordinate gazing towards the bait. Target behaviour: dominant gazing towards the bait. Before the subordinate gazes towards the bait, the dominant gazes towards the bait significantly more than expected from the within-trial shuffled control (peak at time= -3, $r = 0.2381$, $n = 344$; $-\log\text{-likelihood} = 11.1706$, $p < 0.05$).

Cross Correlation, Pair 2 Full Knowledge: When the Subordinate Gazes Towards the Bait, Does the Dominant Gaze Towards the Bait?

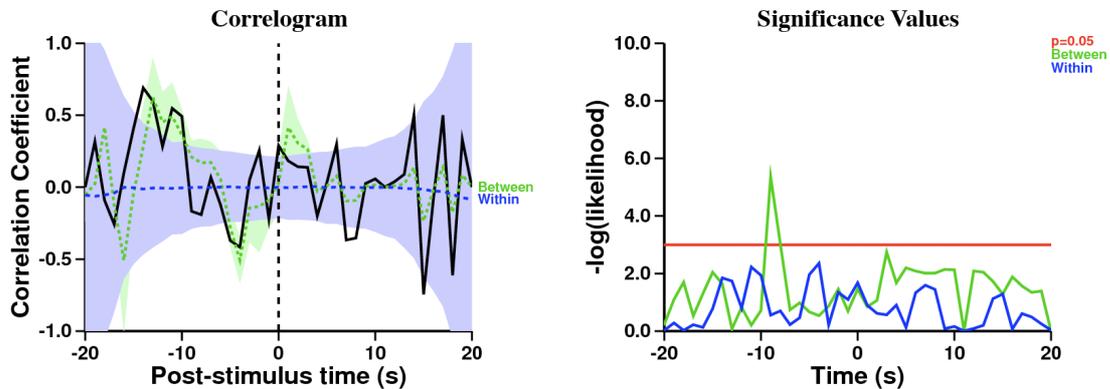


FIGURE 6.16: Referent behaviour: Subordinate gazing towards the bait. Target behaviour: dominant gazing towards the bait. There is no significant relationship between the two variables.

IV. Pair 2 (Reinette and Georgia) Graphs from Phases 1-3

A. Static Gaze Following

1. Phase 1

Cross Correlation, Pair 2 Phase 1: When the Dominant Looks at the Subordinate, Do They Both Gaze Towards the Same Quadrant?

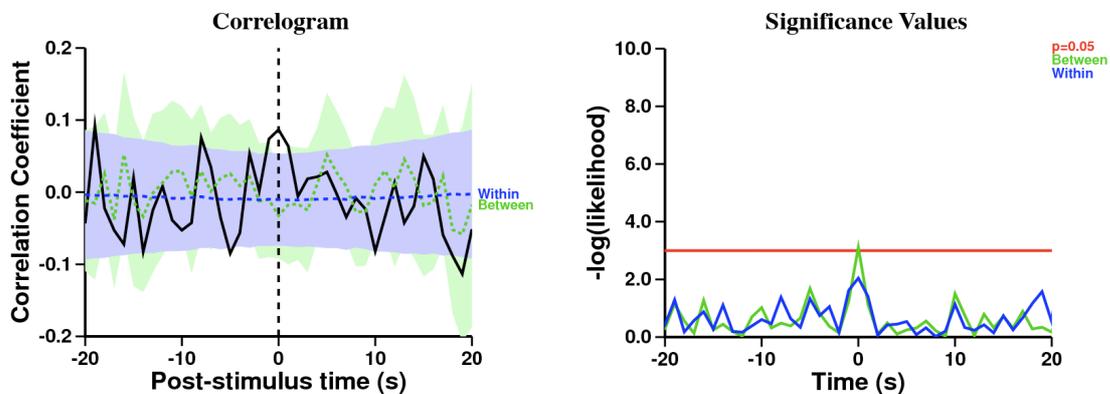


FIGURE 6.17: Referent behaviour: dominant looking at the subordinate. Target behaviour: both chimpanzees gazing towards the same quadrant. At the moment that the dominant looked at the subordinate, both chimpanzees gazed towards the same quadrant (peak at time= 0, $r = 0.0867$, $n = 284$; $-\log\text{-likelihood} = 2.0438$, *ns*).

Cross Correlation, Pair 2 Phase 1: When the Subordinate Looks at the Dominant, Do They Both Gaze Towards the Same Quadrant?

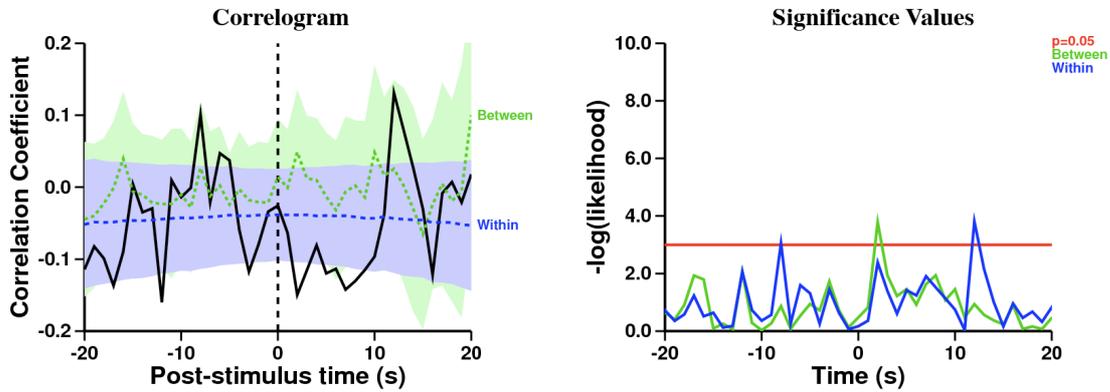


FIGURE 6.18: Referent behaviour: subordinate looking at the dominant. Target behaviour: both chimpanzees gazing towards the same quadrant. Before the subordinate looked at the dominant, both chimpanzees gazed towards the same quadrant (peak at time= -8, $r = 0.1008$, $n = 213$; $-\log\text{-likelihood} = 3.0525$, $p < 0.05$). After the subordinate looked at the dominant, they did not gaze towards the same quadrant (peak at time= +2, $r = -0.1497$, $n = 256$; $-\log\text{-likelihood} = 2.3853$, ns). Ten seconds later, both chimpanzees again gazed towards the same quadrant (peak at time= +12, $r = 0.1312$, $n = 150$; $-\log\text{-likelihood} = 3.8100$, $p < 0.05$).

2. Phase 2

Cross Correlation, Pair 2 Phase 2: When the Dominant Looks at the Subordinate, Do They Both Gaze Towards the Same Quadrant?

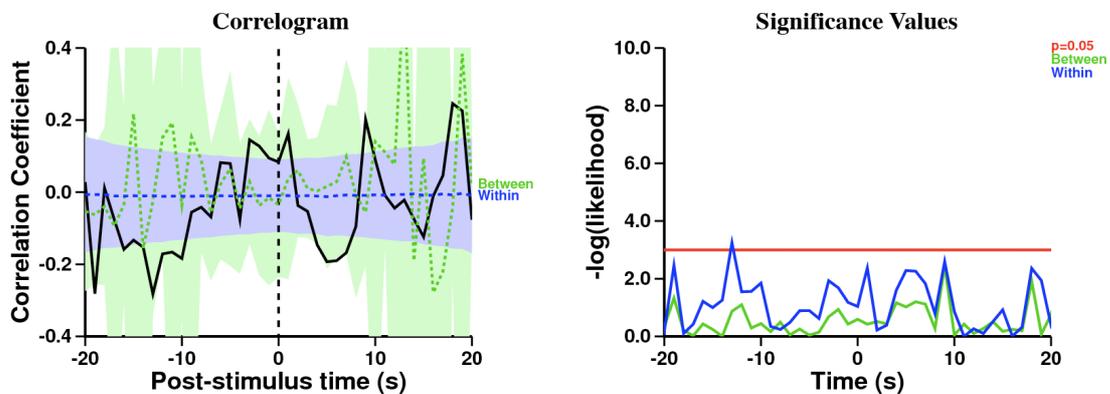


FIGURE 6.19: Referent behaviour: dominant looking at subordinate. Target behaviour: both chimpanzees gazing towards the same quadrant. Before the dominant looked at the subordinate, the chimpanzees gazed towards the same quadrant significantly less than expected from the within-trial shuffled control (peak at time= -13, $r = -0.2827$, $n = 55$; $-\log\text{-likelihood} = 3.2472$, $p < 0.05$). After the dominant looked at the subordinate, both chimpanzees gazed towards the same quadrant; this relationship trends towards being more than expected from the within-trial shuffled control (peak at time= +1, $r = 0.1623$, $n = 120$; $-\log\text{-likelihood} = 2.3719$, ns), but the relationship became negative (peak at time= +5, $r = -0.1930$, $n = 114$; $-\log\text{-likelihood} = 2.2821$, ns), and then positive again (peak at time= +9, $r = 0.2018$, $n = 95$; $-\log\text{-likelihood} = 2.5922$, ns).

Cross Correlation, Pair 2 Phase 2: When the Subordinate Looks at the Dominant, Do They Both Gaze Towards the Same Quadrant?

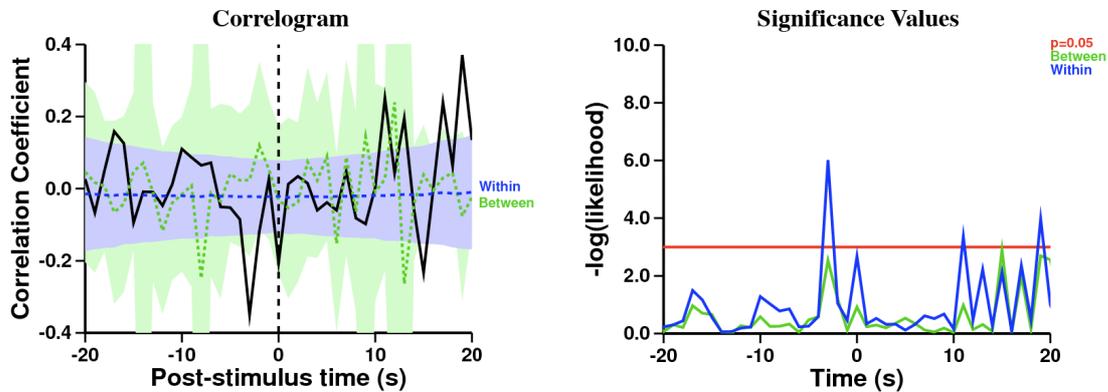


FIGURE 6.20: Referent behaviour: subordinate looking at dominant. Target behaviour: both chimpanzees gazing towards the same quadrant. Before the subordinate looked at the dominant, the chimpanzees gazes towards the same quadrant significantly less than expected from the within-trial shuffled control (peak at time= -3, $r= -0.3499$, $n= 108$; $-\log\text{-likelihood}= 6.0154$, $p<0.05$). Towards the end of the correlogram, the relationship became significantly more than expected from the within-trial shuffled control (peak at time= +19, $r= 0.3708$, $n= 29$; $-\log\text{-likelihood}= 3.9757$, $p<0.05$).

3. Phase 3

Cross Correlation, Pair 2 Phase 3: When the Dominant Looks at the Subordinate, Do They Both Gaze Towards the Same Quadrant?

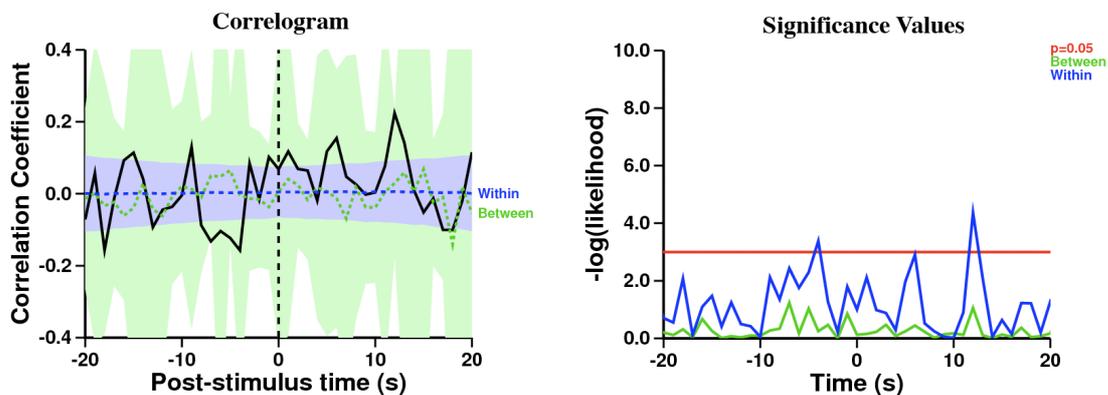


FIGURE 6.21: Referent behaviour: dominant looking at subordinate. Target behaviour: both chimpanzees gazing towards the same quadrant. Before the dominant looked at the subordinate, the chimpanzees did not gaze towards the same quadrant (peak at time= -4, $r= -0.1573$, $n= 178$; $-\log\text{-likelihood}= 3.3815$, $p<0.05$). After the dominant looked at the subordinate, both chimpanzees gazed towards the same quadrant (peak at time= +6, $r= 0.1545$, $n= 189$; $-\log\text{-likelihood}= 2.9068$, *ns*. Peak at time= +12, $r= 0.2240$, $n= 146$; $-\log\text{-likelihood}= 4.3648$, $p<0.05$).

Cross Correlation, Pair 2 Phase 3: When the Subordinate Looks at the Dominant, Do They Both Gaze Towards the Same Quadrant?

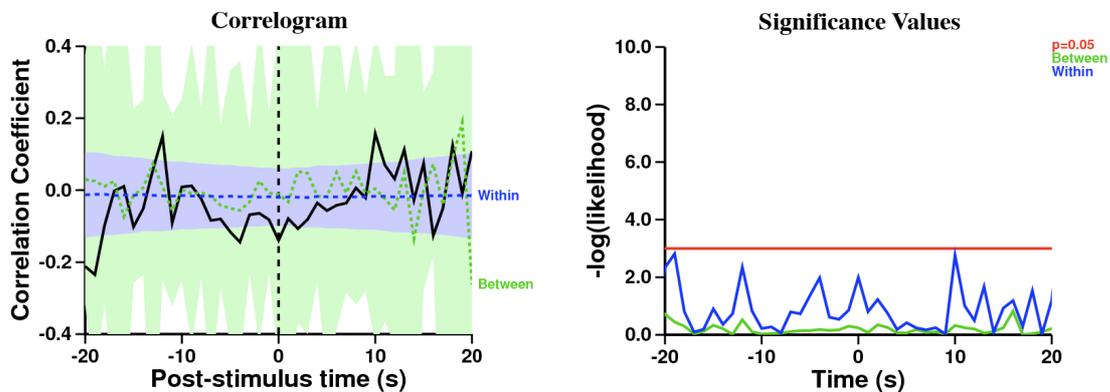


FIGURE 6.22: Referent behaviour: subordinate looking at the dominant. Target behaviour: both chimpanzees gazing towards the same quadrant. At the moment that the subordinate looked at the dominant, the chimpanzees did not gaze towards the same quadrant (peak at time= 0, $r = -0.1398$, $n = 207$; $-\log\text{-likelihood} = 1.9906$, *ns*). Before and after the subordinate looked at the dominant, the relationship of both chimpanzees gazing towards the same quadrant trends towards being more than expected from the within-trial shuffled control (peak at time= -12, $r = 0.1496$, $n = 107$; $-\log\text{-likelihood} = 2.3474$, *ns*. Peak at time= +10, $r = 0.1572$, $n = 121$; $-\log\text{-likelihood} = 2.7569$, *ns*).

B. Following Gaze Onset

1. Phase 1

Cross Correlation, Pair 2 Phase 1: When the Subordinate Changes Gaze Direction in View of the Dominant, Do They Both Gaze Towards the Same Quadrant?

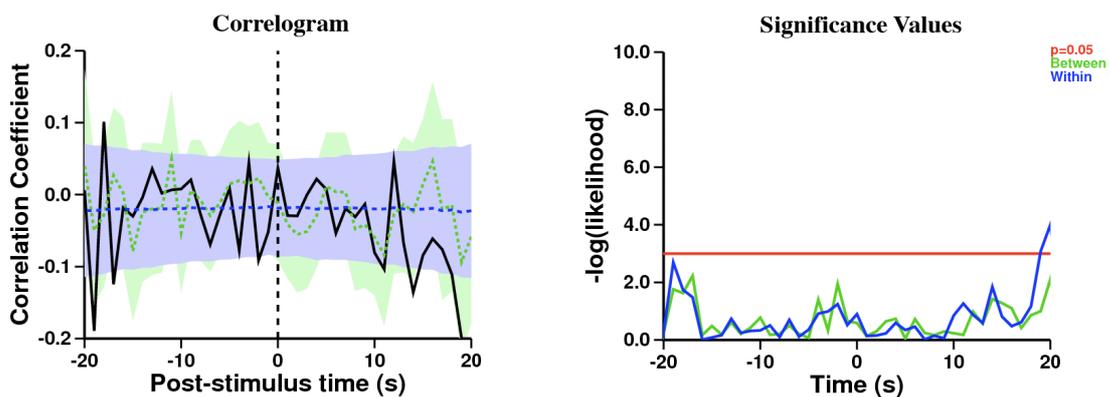


FIGURE 6.23: Referent behaviour: subordinate changes gaze direction in view of the dominant. Target behaviour: both chimpanzees gazing towards the same quadrant. There is no significant relationship between the variables. The relationship became significantly different from the within-trial shuffled control at the end of the correlogram (peak at time= +20, $r = -0.2465$, $n = 89$; $-\log\text{-likelihood} = 4.0000$, $p < 0.05$).

Cross Correlation, Pair 2 Phase 1: When the Dominant Changes Gaze Direction in View of the Subordinate, Do They Both Gaze Towards the Same Quadrant?

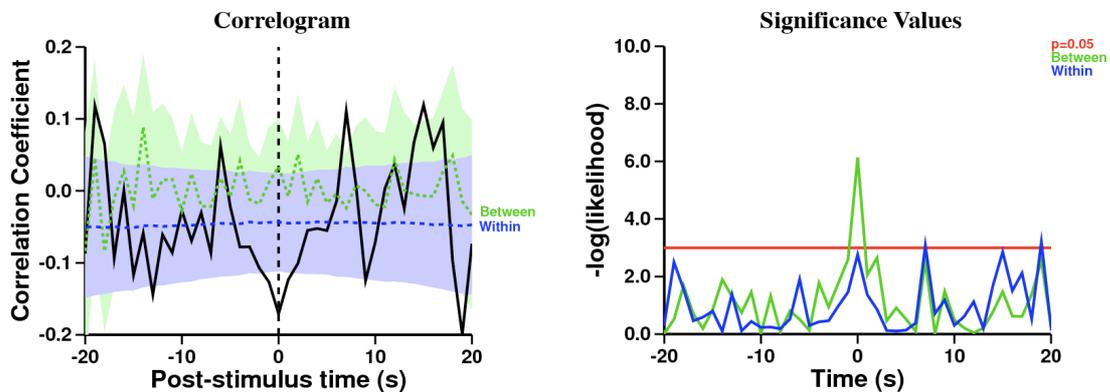


FIGURE 6.24: Referent behaviour: dominant changes gaze in view of the subordinate. Target behaviour: both chimpanzees gazing towards the same quadrant. After the dominant changed gaze direction, the chimpanzees gazed towards the same quadrant; this relationship trends towards being less than expected from the within-trial shuffled control (peak at time= 0, $r = -0.1710$, $n = 276$; $-\log\text{-likelihood} = 2.7618$, ns). After, both chimpanzees gazed towards the same quadrant significantly more than expected from the within-trial shuffled control (peak at time= +7, $r = 0.1107$, $n = 206$; $-\log\text{-likelihood} = 3.0826$, $p < 0.05$).

2. Phase 2

Cross Correlation, Pair 2 Phase 2: When the Subordinate Changes Gaze Direction in View of the Dominant, Do They Both Gaze Towards the Same Quadrant?

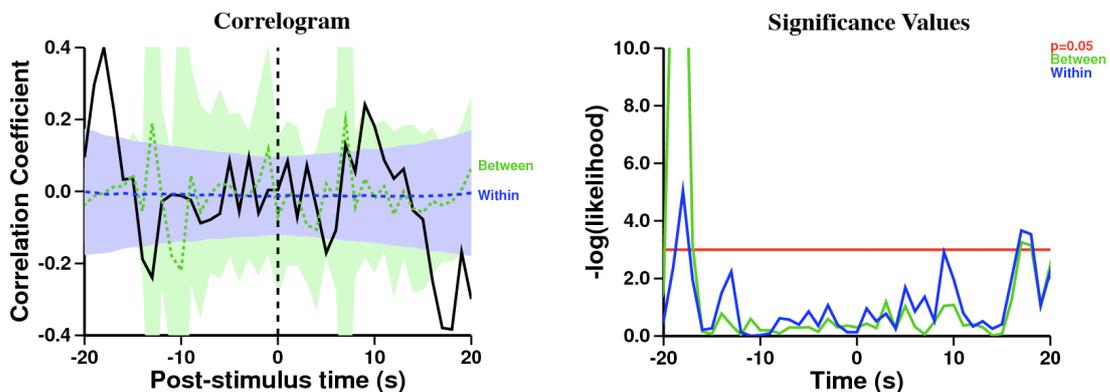


FIGURE 6.25: Referent behaviour: subordinate changes gaze direction in view of the dominant. Target behaviour: both chimpanzees gazing towards the same quadrant. After the subordinate changed her gaze, both chimpanzees gazed towards the same quadrant (peak at time= +9, $r = 0.2411$, $n = 70$; $-\log\text{-likelihood} = 2.9128$, ns). Before the subordinate changed her gaze the chimpanzees gazed towards the same quadrant (peak at time= -18, $r = 0.4743$, $n = 31$; $-\log\text{-likelihood} = 5.0397$, $p < 0.05$). After the subordinate changed her gaze, the chimpanzees did not gaze towards the same quadrant (peak at time= +17, $r = -0.3795$, $n = 32$; $-\log\text{-likelihood} = 3.6647$, $p < 0.05$).

Correlation Coefficient, Pair 2 Phase 2: When the Dominant Changes Gaze Direction in View of the Subordinate, Do They Both Gaze Towards the Same Quadrant?

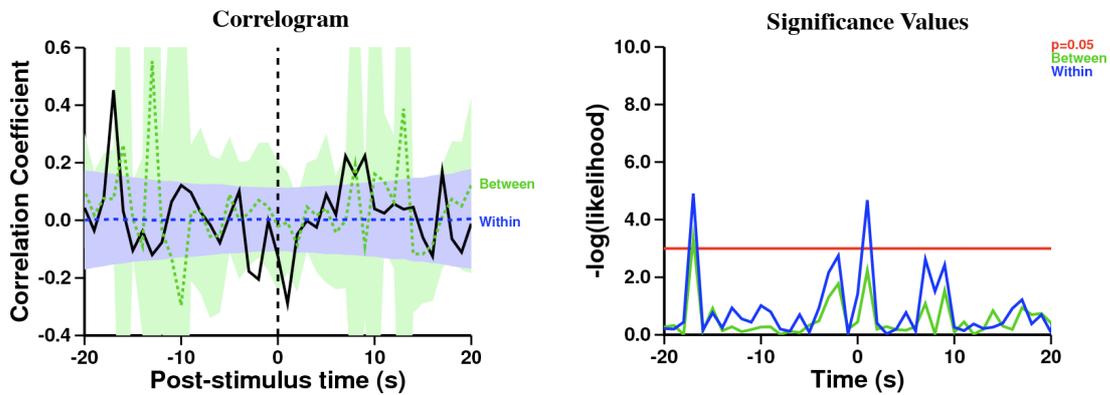


FIGURE 6.26: Referent behaviour: dominant changes gaze direction in view of the subordinate. Target behaviour: both chimpanzees gazing towards the same quadrant. After the dominant changed her gaze, the chimpanzees did not gaze towards the same quadrant (peak at time= +1, $r = -0.2896$, $n = 116$; $-\log\text{-likelihood} = 4.6803$, $p < 0.05$). Later, the chimpanzees gazed towards the same quadrant; this relationship trends towards being more than expected from the within-trial shuffled control (peak at time= +7, $r = 0.2233$, $n = 86$; $-\log\text{-likelihood} = 2.6229$, ns). Before the dominant changed her gaze direction, both chimpanzees gazed towards the same quadrant (peak at time= -17, $r = 0.4526$, $n = 36$; $-\log\text{-likelihood} = 4.9095$, $p < 0.05$).

3. Phase 3

Cross Correlation, Pair 2 Phase 3: When the Subordinate Changes Gaze Direction in View of the Dominant, Do They Both Gaze Towards the Same Quadrant?

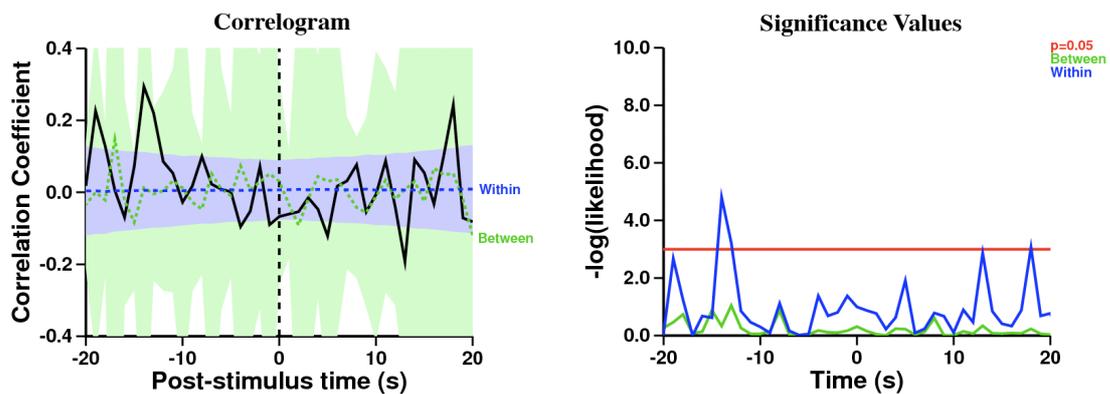


FIGURE 6.27: Referent behaviour: subordinate changes gaze in view of the dominant. Target behaviour: both chimpanzees gazing towards the same quadrant. Before the subordinate changed her gaze, both chimpanzees gazed towards the same quadrant (peak at time= -14, $r = 0.2940$, $n = 82$; $-\log\text{-likelihood} = 4.8041$, $p < 0.05$). After the subordinate changed her gaze, the chimpanzees were unlikely to gaze towards the same quadrant (peak at time= +13, $r = -0.1922$, $n = 87$; $-\log\text{-likelihood} = 2.8678$, ns), later they both gazed towards the same quadrant significantly more than expected from the within-trial shuffled control (peak at time= +18, $r = 0.2427$, $n = 63$; $-\log\text{-likelihood} = 3.0658$, $p < 0.05$).

Cross Correlation, Pair 2 Phase 3: When the Dominant Changes Gaze Direction in View of the Subordinate, Do They Both Gaze Towards the Same Quadrant?

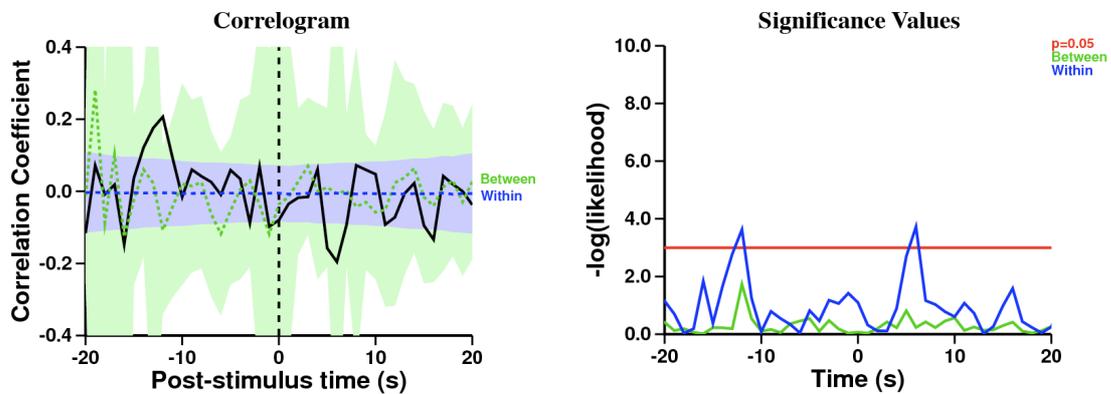


FIGURE 6.28: Referent behaviour: dominant changes gaze in view of the subordinate. Target behaviour: both chimpanzees gazing towards the same quadrant. Before the dominant changed her gaze, both chimpanzees gazed towards the same quadrant significantly more than expected from the within-trial shuffled control (peak at time= -12, $r = 0.2068$, $n = 119$; $-\log\text{-likelihood} = 3.6269$, $p < 0.05$). After the dominant changed her gaze, the chimpanzees did not gaze towards the same quadrant (peak at time= +6, $r = -0.1957$, $n = 159$; $-\log\text{-likelihood} = 3.7245$, $p < 0.05$).

Appendix to Chapter 7: *Approach, Footsteps, Convergence, Static* gaze graphs for *Unequal Rewards*; All *Unequal Rewards* analyses with dominant as referent

Missy & Rita

I. *Approach*

II. *Footsteps*

III. *Convergence*

IV. *Static Gaze*

V. *Unequal Rewards* analyses with dominant as referent

Reinette & Georgia

I. *Approach*

II. *Footsteps*

III. *Convergence*

IV. *Static Gaze*

V. *Unequal Rewards* analyses with dominant as referent

Missy & Rita

I. *Approach*

Cross Correlation, Pair 1 *Unequal Rewards*: When the Subordinate Walks Towards the Banana, Does the Dominant *Approach* the Subordinate?

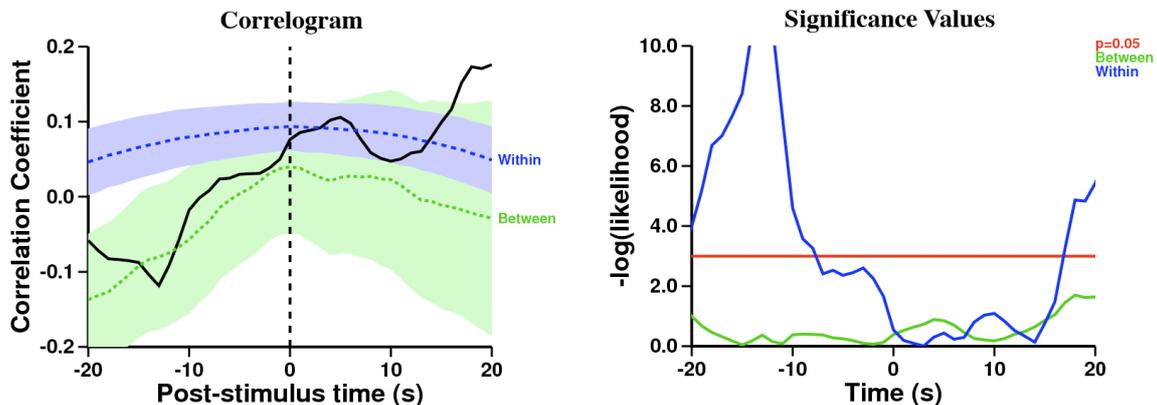


FIGURE 7.1: Referent behaviour: subordinate walks towards the banana. Target behaviour: dominant *approaches* the subordinate. Before the subordinate walked towards the banana, the dominant *approached* her significantly less than expected from the within-trial shuffled control (peak at time= -13, $r = -0.1185$, $n = 643$; $-\log\text{-likelihood} = 12.9966$, $p < 0.05$). Many seconds after the subordinate walked towards the banana, the dominant *approached* (peak at time= +20, $r = 0.1759$, $n = 508$; $-\log\text{-likelihood} = 5.4247$, $p < 0.05$)

Cross Correlation, Pair 1 *Unequal Rewards*: When the Subordinate Walks Towards the Cucumber, Does the Dominant *Approach* the Subordinate?

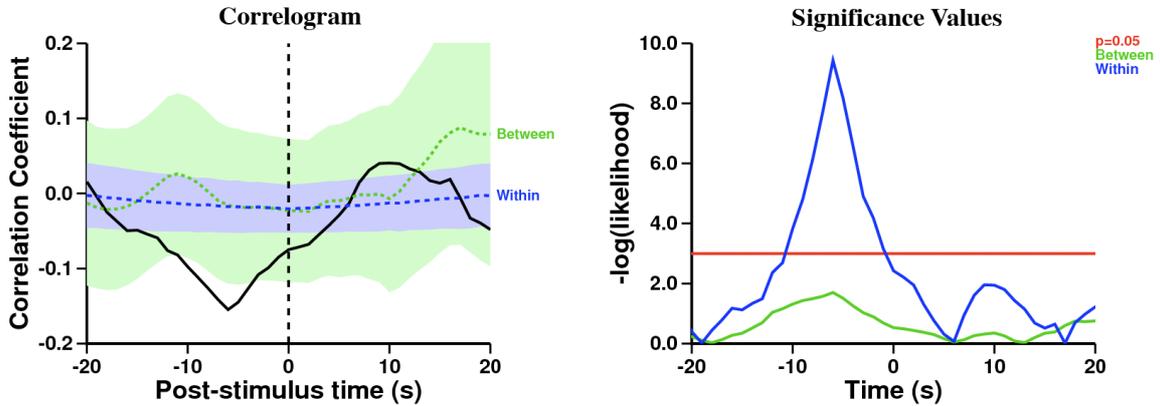


FIGURE 7.2: Referent behaviour: subordinate walking towards the cucumber. Target behaviour: dominant *approaches* the subordinate. Before the subordinate walked towards the cucumber, the dominant was significantly unlikely to *approach* (peak at time= -6, $r = -0.1548$, $n = 778$; $-\log\text{-likelihood} = 9.4326$, $p < 0.05$). After the subordinate walked towards the cucumber, the relationship of the dominant *approaching* only trended towards being more than expected from the within-trial shuffled control (peak at time= +9, $r = 0.0399$, $n = 709$; $-\log\text{-likelihood} = 1.9570$, *ns*).

Cross Correlation, Pair 1 *Unequal Rewards*: When the Subordinate Walks Towards the Banana, Does the Subordinate *Approach* the Dominant?

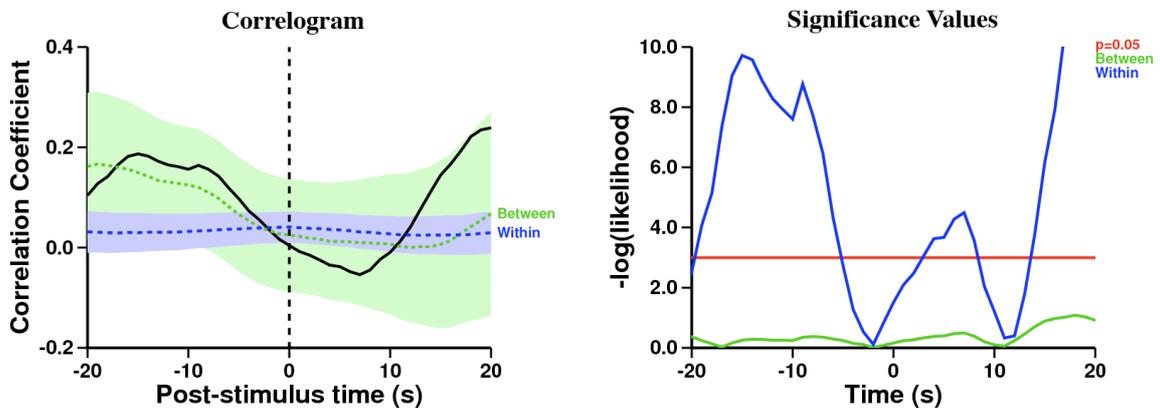


FIGURE 7.3: Referent behaviour: subordinate walks towards the banana. Target behaviour: subordinate *approaches* the dominant. Before the subordinate walked towards the banana, she *approached* the dominant (peak at time= -15, $r = 0.1868$, $n = 609$; $-\log\text{-likelihood} = 9.7207$, $p < 0.05$). Shortly after the subordinate began walking towards the banana, she did not *approach* the dominant (peak at time= +7, $r = -0.0541$, $n = 751$; $-\log\text{-likelihood} = 4.4935$, $p < 0.05$), but a few seconds later the subordinate again approached the dominant (peak at time= +20, $r = 0.2387$, $n = 508$; $-\log\text{-likelihood} = 14.0373$, $p < 0.05$).

Cross Correlation, Pair 1 *Unequal Rewards*: When the Subordinate Walks Towards the Cucumber, Does the Subordinate Approach the Dominant?

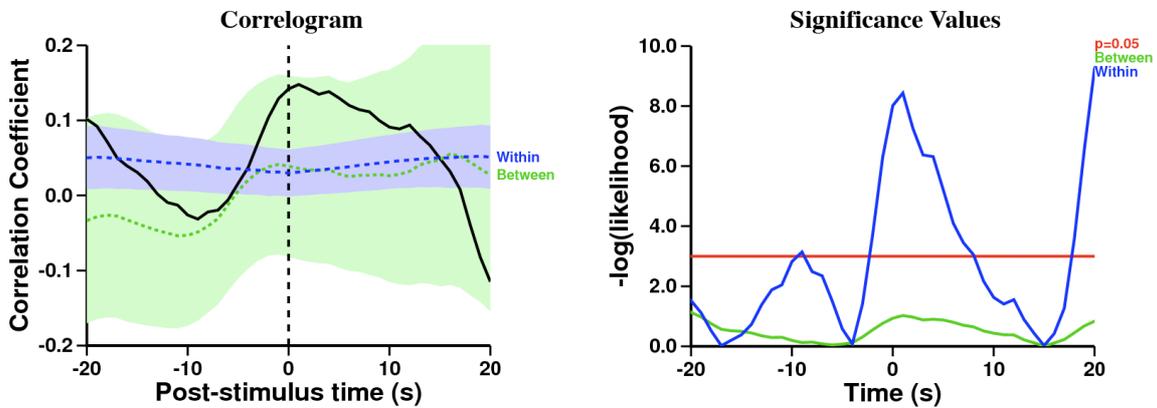


FIGURE 7.4: Referent behaviour: subordinate walks towards the cucumber. Target behaviour: subordinate *approaches* the dominant. Before the subordinate walks towards the cucumber, she does not *approach* the dominant (peak at time= -9, $r = -0.0315$, $n = 718$; $-\log\text{-likelihood} = 3.1417$, $p < 0.05$). After the subordinate began to walk towards the cucumber, she *approached* the dominant (peak at time= +1, $r = 0.1478$, $n = 877$; $-\log\text{-likelihood} = 8.4335$, $p < 0.05$). Many seconds later, the subordinate does not *approach* the dominant (peak at time= +20, $r = -0.1149$, $n = 508$; $-\log\text{-likelihood} = 9.2484$, $p < 0.05$).

Cross Correlation, Pair 1 *Unequal Rewards*: When the Dominant Walks Towards the Banana, Does the Dominant Approach the Subordinate?

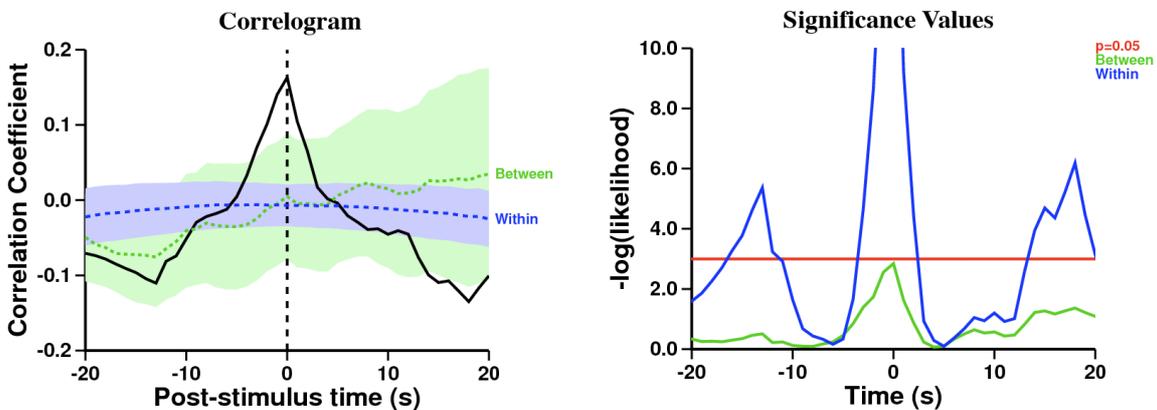


FIGURE 7.5: Referent behaviour: dominant walks towards the banana. Target behaviour: dominant *approaches* the subordinate. At the moment the dominant walked towards the banana, she *approached* the subordinate (peak at time= 0, $r = 0.1631$, $n = 898$; $-\log\text{-likelihood} = 20.7847$, $p < 0.05$). Both before and after the dominant walked towards the banana, she *approached* the subordinate significantly less than expected from the within-trial shuffled control (peak at time= -13, $r = -0.1104$, $n = 627$; $-\log\text{-likelihood} = 5.3649$, $p < 0.05$. time= +18, $r = -0.1350$, $n = 601$; $-\log\text{-likelihood} = 6.1872$, $p < 0.05$).

Cross Correlation, Pair 1 *Unequal Rewards*: When the Dominant Walks Towards the Cucumber, Does the Dominant Approach the Subordinate?

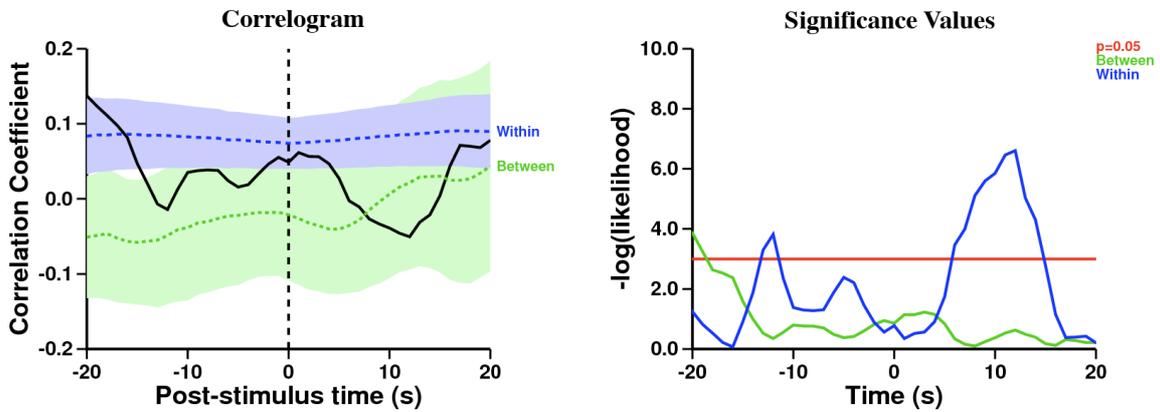


FIGURE 7.6: Referent behaviour: dominant walks towards the cucumber. Target behaviour: dominant *approaches* the subordinate. Both before and after the dominant walked towards the cucumber, she did not *approach* the subordinate (time= -12, $r = -0.0142$, $n = 647$; $-\log\text{-likelihood} = 3.8170$, $p < 0.05$. time= +12, $r = -0.0505$, $n = 714$; $-\log\text{-likelihood} = 6.6064$, $p < 0.05$)

Cross Correlation, Pair 1 *Unequal Rewards*: When the Dominant Walks Towards the Banana, Does the Subordinate Approach the Dominant?

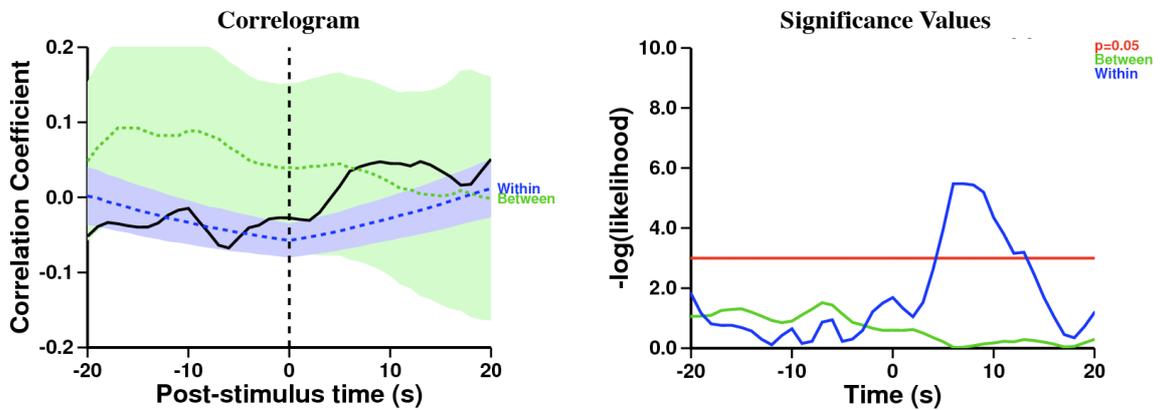


FIGURE 7.7: Referent behaviour: dominant walks towards the banana. Target behaviour: subordinate *approaches* the dominant. After the dominant walked towards the banana, the subordinate *approached* her (peak at time= + 7, $r = 0.0408$, $n = 821$; $-\log\text{-likelihood} = 5.4773$, $p < 0.05$)

Cross Correlation, Pair 1 *Unequal Rewards*: When the Dominant Walks Towards the Cucumber, Does the Subordinate *Approach* the Dominant?

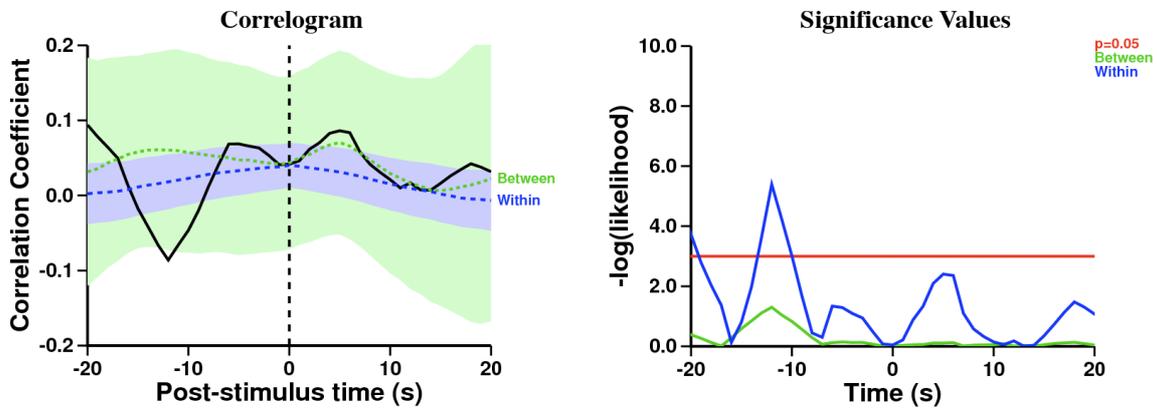


FIGURE 7.8: Referent behaviour: dominant walks towards the cucumber. Target behaviour: subordinate *approaches* the dominant. Before the dominant walked towards the cucumber, the subordinate was significantly unlikely to *approach* the dominant (peak at time= -12, $r = -0.0861$, $n = 647$; $-\log\text{-likelihood} = 5.3918$, $p < 0.05$). After the dominant walked towards the cucumber, the relationship of the subordinate *approaching* her only trended towards being more than expected from the within-trial shuffled control (peak at time= +5, $r = 0.0862$, $n = 856$; $-\log\text{-likelihood} = 2.4039$, ns)

II. Footsteps

Cross Correlation, Pair 1 *Unequal Rewards*: When the Subordinate Walks Towards the Banana, Does the Subordinate Follow in the Dominant's *Footsteps*?

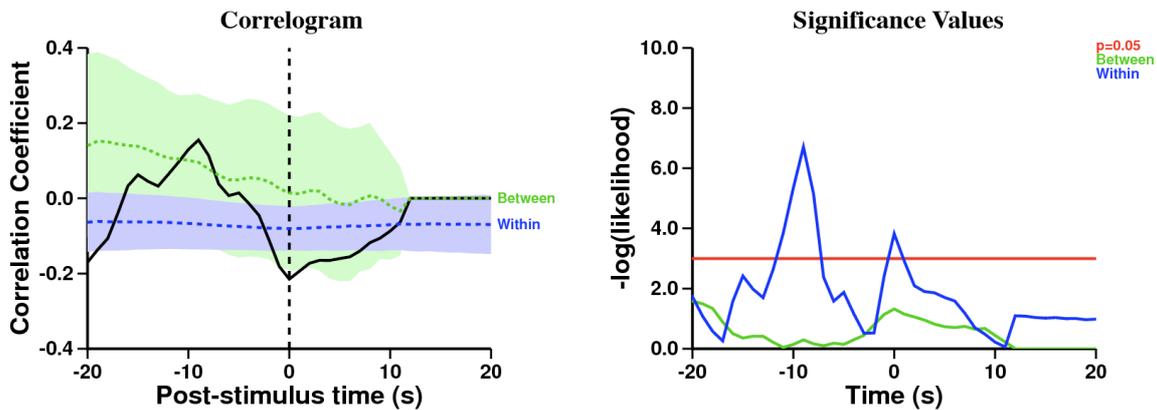


FIGURE 7.9: Referent behaviour: subordinate walks towards the banana. Target behaviour: subordinate walks in dominant's *footsteps*. The subordinate followed in the dominant's *footsteps* before, but not after, she walked towards the banana (time= -9, $r = 0.1551$, $n = 170$; $-\log\text{-likelihood} = 6.7087$, $p < 0.05$. time= 0, $r = -0.2149$, $n = 201$; $-\log\text{-likelihood} = 3.8232$, $p < 0.05$)

Cross Correlation, Pair 1 *Unequal Rewards*: When the Subordinate Walks Towards the Cucumber, Does the Subordinate Follow in the Dominant's *Footsteps*?

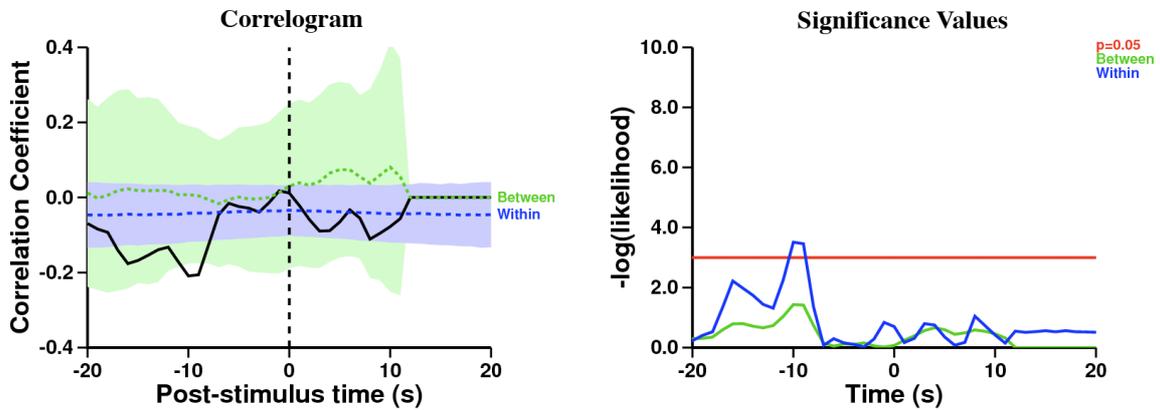


FIGURE 7.10: Referent behaviour: subordinate walks towards the cucumber. Target behaviour: subordinate walks in dominant's *footsteps*. Before the subordinate walked towards the cucumber, she did not follow in the dominant's *footsteps* (peak at time= -10, $r = -0.2091$, $n = 168$; $-\log\text{-likelihood} = 3.5094$, $p < 0.05$). Afterward, there was no relationship.

Cross Correlation, Pair 1 *Unequal Rewards*: When the Dominant Walks Towards the Banana, Does the Subordinate Follow in the Dominant's *Footsteps*?

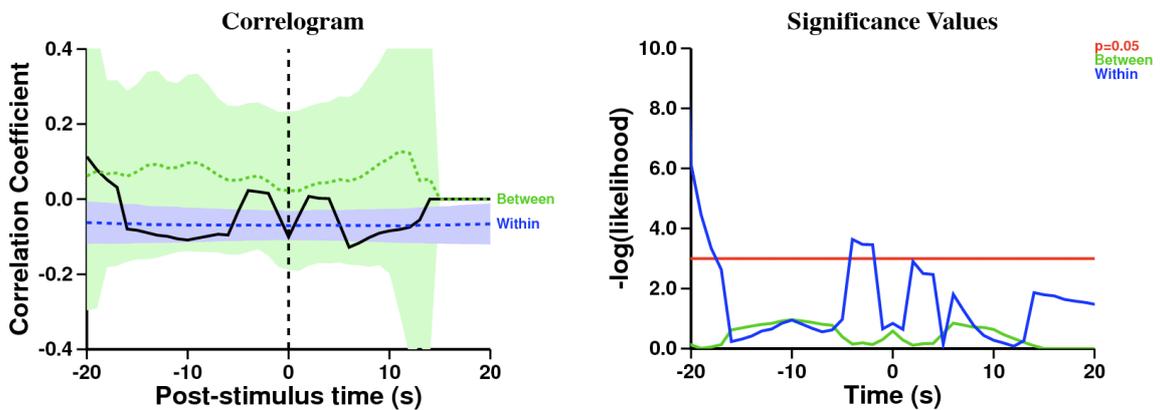


FIGURE 7.11: Referent behaviour: dominant walks towards the banana. Target behaviour: subordinate walks in dominant's *footsteps*. When the dominant walked towards the banana, the subordinate walked in her *footsteps* briefly before and after (time= -4, $r = 0.0229$, $n = 187$; $-\log\text{-likelihood} = 3.6365$, $p < 0.05$. time= +2, $r = 0.0074$, $n = 200$; $-\log\text{-likelihood} = 2.8994$, ns)

Cross Correlation, Pair 1 *Unequal Rewards*: When the Dominant Walks Towards the Cucumber, Does the Subordinate Follow in the Dominant's *Footsteps*?

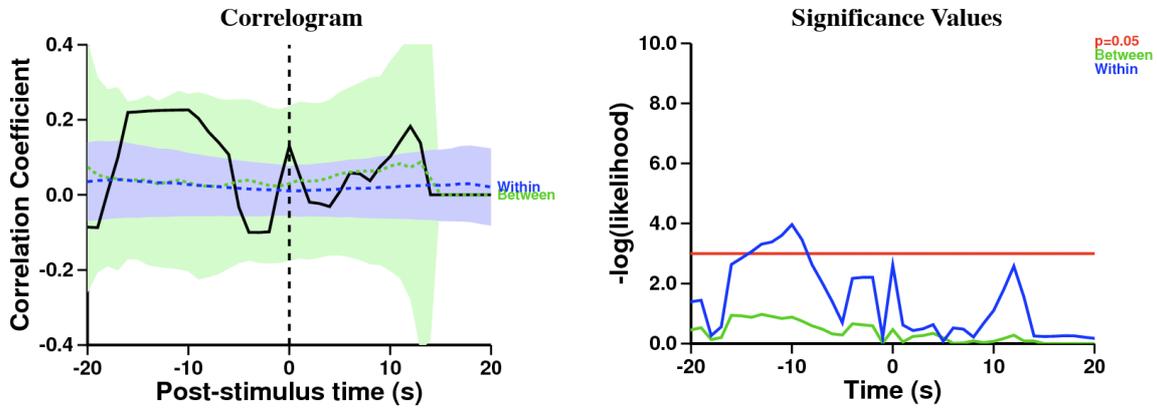


FIGURE 7.12: Referent behaviour: dominant walks towards cucumber. Target behaviour: subordinate walks in dominant's *footsteps*. Before the dominant walked towards the cucumber, the subordinate followed in her *footsteps* (peak at time= -10, $r = 0.2264$, $n = 168$; $-\log\text{-likelihood} = 3.9642$, $p < 0.05$). At the moment the dominant walked towards the cucumber, the subordinate followed in her *footsteps* (time= 0, $r = 0.1300$, $n = 201$; $-\log\text{-likelihood} = 2.6148$, ns). Later the subordinate followed in the dominant's *footsteps* (time= +12, $r = 0.1825$, $n = 121$; $-\log\text{-likelihood} = 2.5772$, ns)

III. Convergence

Cross Correlation, Pair 1 *Unequal Rewards*: When the Subordinate Walks Towards the Banana, Do Both Chimpanzees *Converge*?

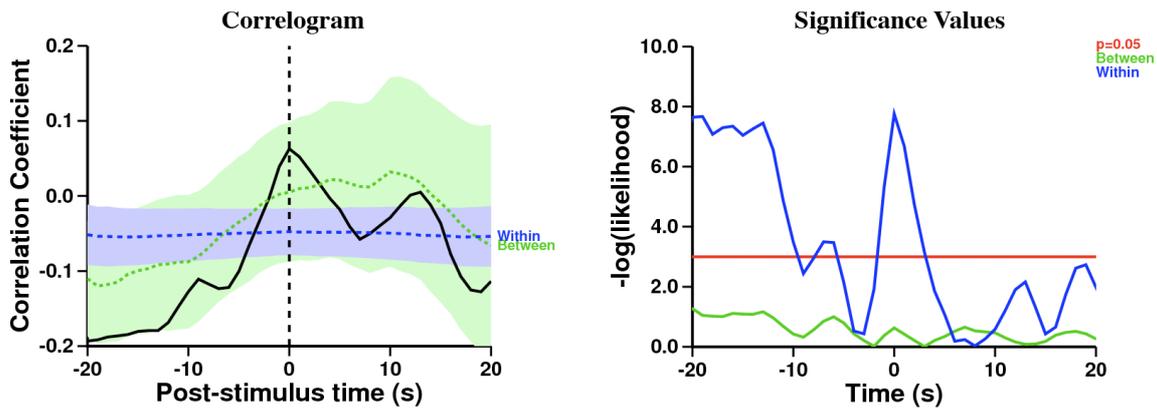


FIGURE 7.13: Referent behaviour: subordinate walks towards the banana. Target behaviour: both chimpanzees *converge*. Before the subordinate walked towards the banana, the chimpanzees did not *converge* (time= -19, $r = -0.1917$, $n = 548$; $-\log\text{-likelihood} = 7.6694$, $p < 0.05$). At the moment the subordinate walked towards the banana, the chimpanzees *converged* (time= 0, $r = 0.0628$, $n = 898$; $-\log\text{-likelihood} = 7.7558$, $p < 0.05$). Many seconds later, they did not (time= +19, $r = -0.1277$, $n = 524$; $-\log\text{-likelihood} = 2.7327$, ns)

Cross Correlation, Pair 1 *Unequal Rewards*: When the Subordinate Walks Towards the Cucumber, Do Both Chimpanzees Converge?

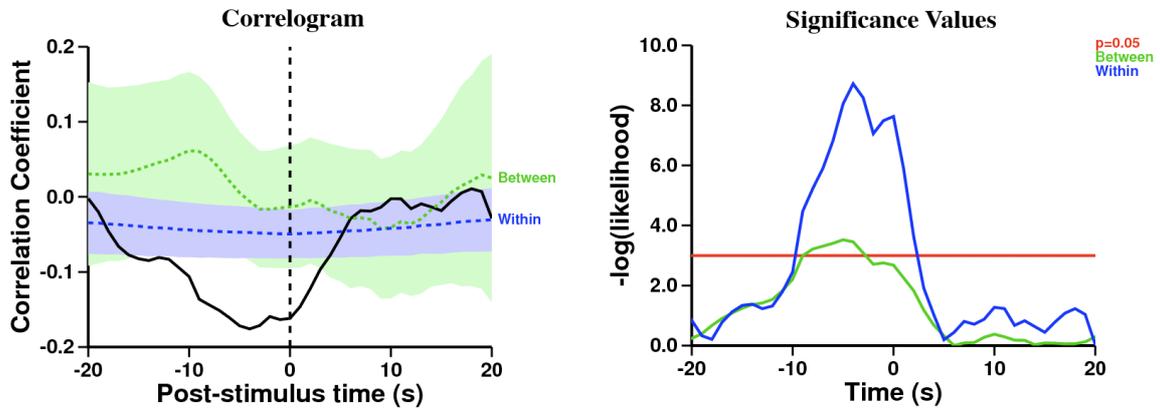


FIGURE 7.14: Referent behaviour: subordinate walks towards the cucumber. Target behaviour: both chimpanzees *converge*. Before the subordinate walked towards the cucumber, the chimpanzees did not *converge* (peak at time= -4, $r = -0.1759$, $n = 818$; $-\log\text{-likelihood} = 8.7201$ $p < 0.05$). After, there was no relationship.

Cross Correlation, Pair 1 *Unequal Rewards*: When the Dominant Walks Towards the Banana, Do Both Chimpanzees Converge?

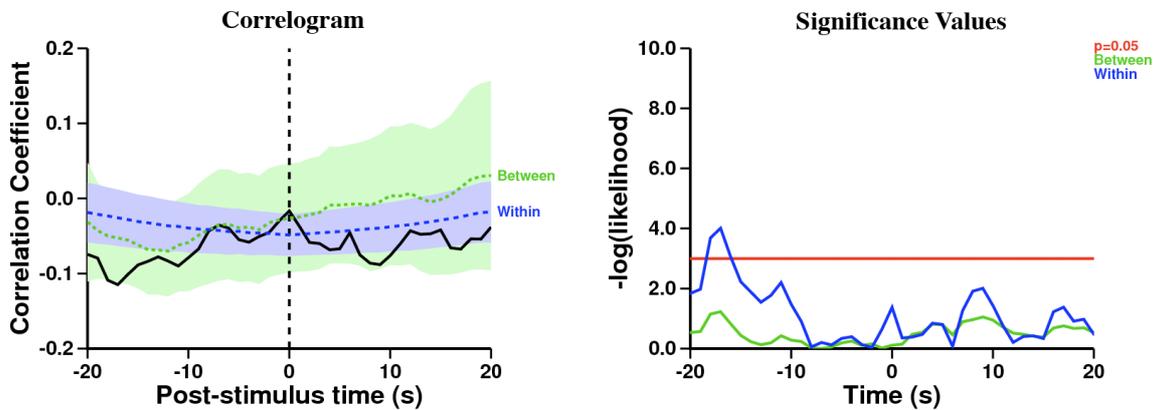


FIGURE 7.15: Referent behaviour: dominant walks towards the banana. Target behaviour: both chimpanzees *converge*. Before the dominant walked towards the banana, the chimpanzees did not *converge* (time= -17, $r = -0.1149$, $n = 559$; $-\log\text{-likelihood} = 4.0095$, $p < 0.05$). Afterward there was no relationship.

Cross Correlation, Pair 1 *Unequal Rewards*: When the Dominant Walks Towards the Cucumber, Do Both Chimpanzees Converge?

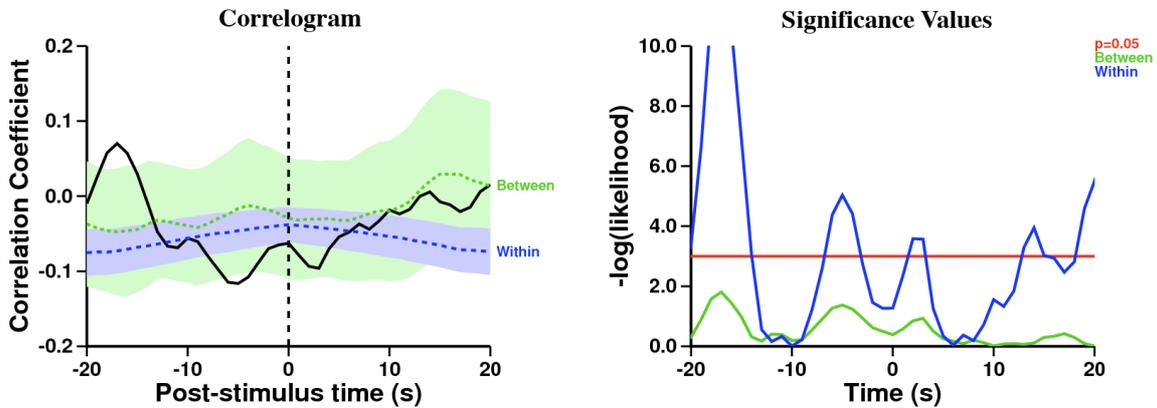


FIGURE 7.16: Referent behaviour: dominant walks towards cucumber. Target behaviour: both chimpanzees *converge*. Shortly before and after the dominant walked towards the cucumber, the chimpanzees did not *converge* (peak at time= -5, $r = -0.1164$, $n = 792$; $-\log$ -likelihood= 5.0359, $p < 0.05$). Long before and long after the dominant began walking towards the cucumber, the chimpanzees did *converge* (time= -17, $r = 0.0701$, $n = 559$; $-\log$ -likelihood= 12.9586, $p < 0.05$. time= +20, $r = 0.0152$, $n = 568$; $-\log$ -likelihood= 5.5011, $p < 0.05$)

IV. *Static Gaze*

Cross Correlation, Pair 1 *Unequal Rewards*: When the Dominant Follows the Subordinate's *Static Gaze*, Does the Dominant Gaze Towards the Banana?

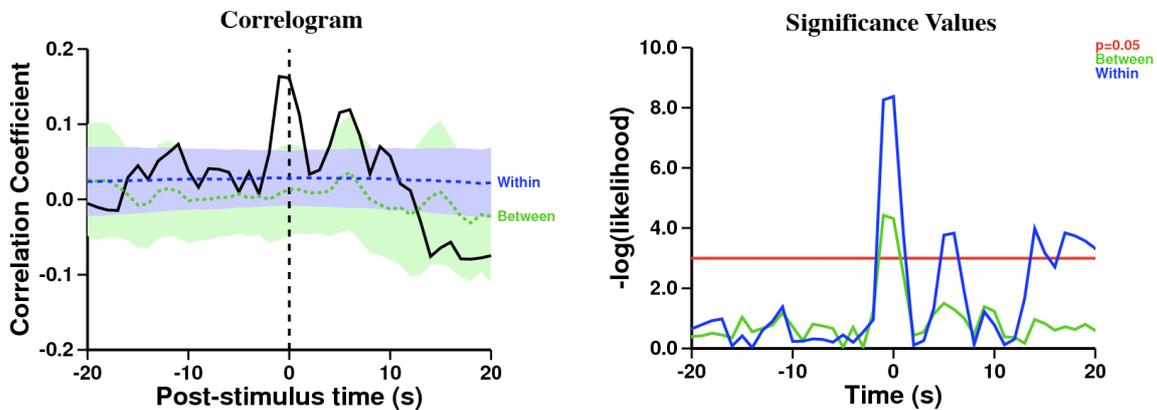


FIGURE 7.17: Referent behaviour: dominant follows subordinate's *static gaze*. Target behaviour: dominant gazes towards the banana. At the moment that the dominant follows the subordinate's *static gaze*, the dominant gazes towards the banana significantly more than expected from the within-trial shuffled control (time= 0, $r = 0.1614$, $n = 880$; $-\log$ -likelihood= 8.3742, $p < 0.05$). Many seconds later, the dominant does not gaze towards the banana (time= +17, $r = -0.0791$, $n = 566$; $-\log$ -likelihood= 3.8400, $p < 0.05$).

Cross Correlation, Pair 1 *Unequal Rewards*: When the Dominant Follows the Subordinate's *Static* Gaze, Does the Dominant Gaze Towards the Cucumber?

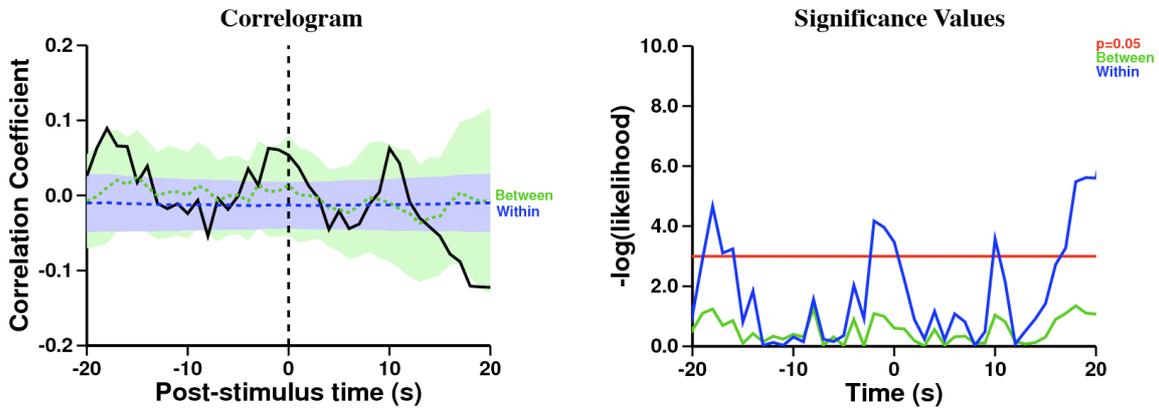


FIGURE 7.18: Referent behaviour: dominant follows subordinate's *static* gaze. Target behaviour: dominant gazes towards the cucumber. Shortly before the dominant follows the subordinate's *static* gaze, she gazes towards the cucumber (time= -2, $r = 0.0628$, $n = 880$; $-\log\text{-likelihood} = 4.1736$, $p < 0.05$). after the dominant follows the subordinate's *static* gaze, she gazes towards the cucumber (time= +10, $r = 0.0628$, $n = 690$; $-\log\text{-likelihood} = 3.5736$, $p < 0.05$).

Cross Correlation, Pair 1 *Unequal Rewards*: When the Dominant Follows the Subordinate's *Static* Gaze, Does the Subordinate Gaze Towards the Banana?

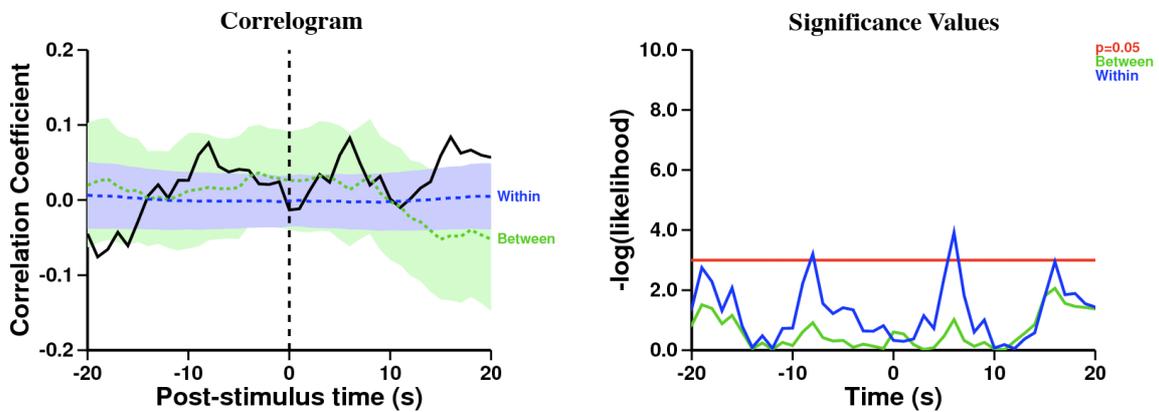


FIGURE 7.19: Referent behaviour: dominant follows subordinate's *static* gaze. Target behaviour: subordinate gazes towards the banana. Several seconds before and after the dominant follows the subordinate's *static* gaze, the subordinate gazes towards the banana (time= -8, $r = 0.0761$, $n = 736$; $-\log\text{-likelihood} = 3.2020$, $p < 0.05$. time= +6, $r = 0.0827$, $n = 768$; $-\log\text{-likelihood} = 3.9176$, $p < 0.05$).

Cross Correlation, Pair 1 *Unequal Rewards*: When the Dominant Follows the Subordinate's *Static* Gaze, Does the Subordinate Gaze Towards the Cucumber?

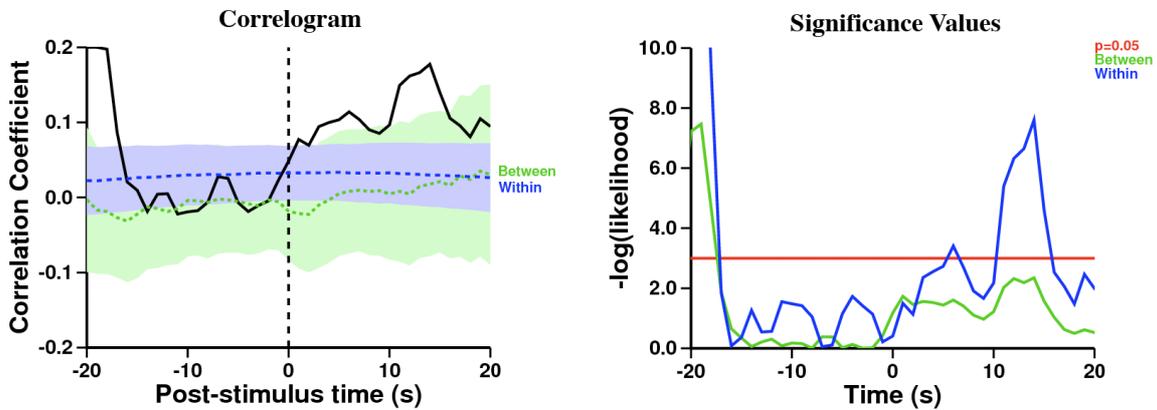


FIGURE 7.20: Referent behaviour: dominant follows the subordinate's *static* gaze. Target behaviour: subordinate gazes towards the cucumber. Before the dominant followed the subordinate's *static* gaze, the subordinate did not gaze towards the cucumber (time= -20, $r= 0.3247$, $n= 514$; $-\log\text{-likelihood}= 22.9998$, $p<0.05$). Several seconds after the dominant followed the subordinate's *static* gaze, the subordinate gazed towards the cucumber (time= +14, $r= 0.1775$, $n= 628$; $-\log\text{-likelihood}= 7.6043$, $p<0.05$)

Cross Correlation, Pair 1 *Unequal Rewards*: When the Subordinate Follows the Dominant's *Static* Gaze, Does the Dominant Gaze Towards the Banana?

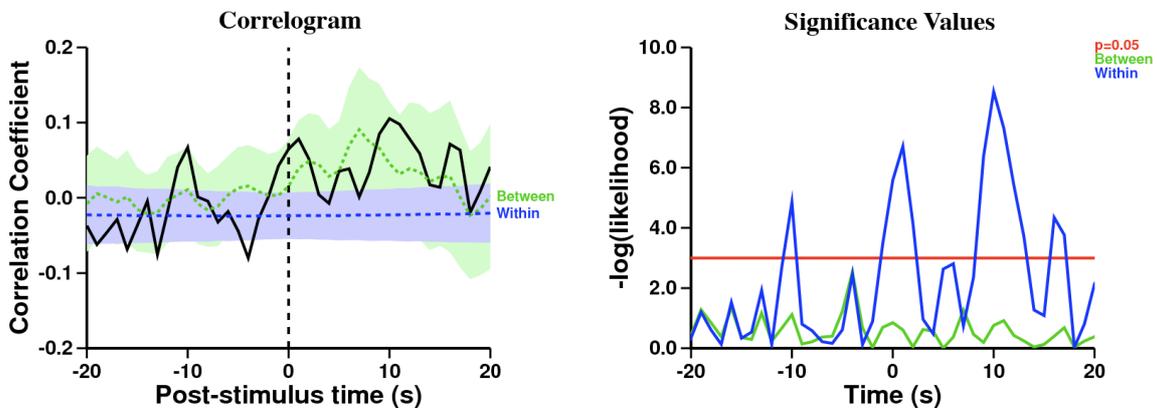


FIGURE 7.21: Referent behaviour: subordinate follows the dominant's *static* gaze. Target behaviour: dominant gazes towards the banana. Several seconds before, at the moment, and several seconds after the subordinate followed the dominant's *static* gaze, the dominant gazed towards the banana (time= -10, $r= 0.0670$, $n= 765$; $-\log\text{-likelihood}= 4.8564$, $p<0.05$. time= +1, $r= 0.0782$, $n= 876$; $-\log\text{-likelihood}= 6.7104$, $p<0.05$. time= +10, $r= 0.1053$, $n= 688$; $-\log\text{-likelihood}= 8.5307$, $p<0.05$)

Cross Correlation, Pair 1 *Unequal Rewards*: When the Subordinate Follows the Dominant's *Static* Gaze, Does the Dominant Gaze Towards the Cucumber?

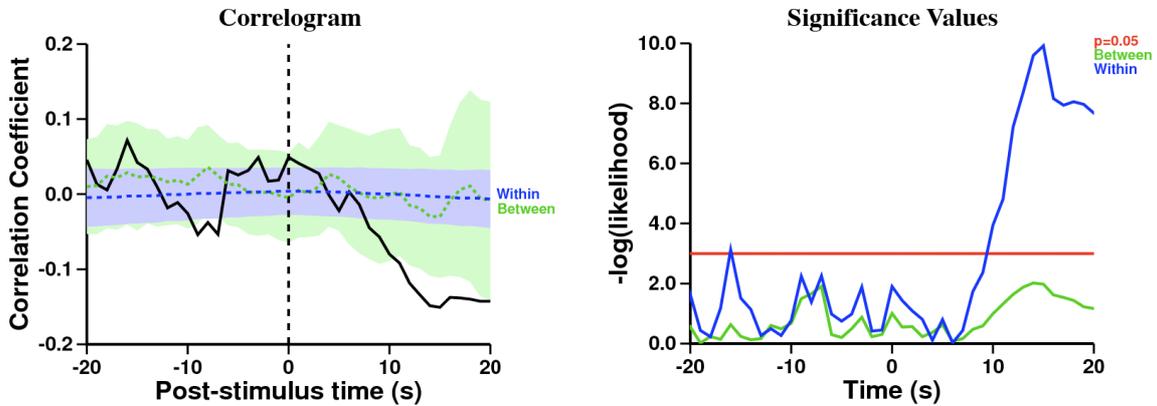


FIGURE 7.22: Referent behaviour: subordinate follows the dominant's *static* gaze. Target behaviour: dominant gazes towards cucumber. After the subordinate followed the dominant's *static* gaze, the dominant gazed towards the cucumber significantly less than expected from the within-trial shuffled control (time= +15, $r = -0.1508$, $n = 595$; $-\log\text{-likelihood} = 9.9170$, $p < 0.05$).

Cross Correlation, Pair 1 *Unequal Rewards*: When the Subordinate Follows the Dominant's *Static* Gaze, Does the Subordinate Gaze Towards the Banana?

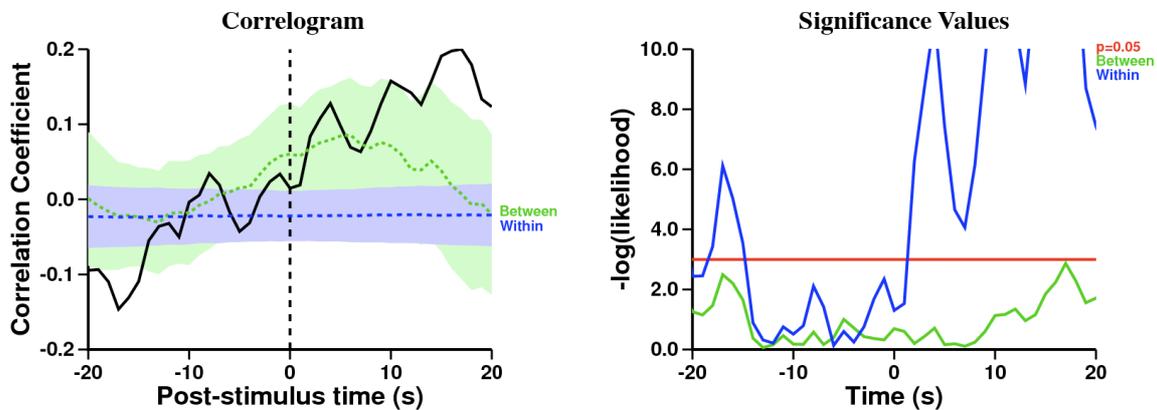


FIGURE 7.23: Referent behaviour: subordinate follows dominant's *static* gaze. Target behaviour: subordinate gazes towards banana. Before the subordinate followed the dominant's *static* gaze, the subordinate did not gaze towards the banana (time= -17, $r = -0.1464$, $n = 562$; $-\log\text{-likelihood} = 6.1164$, $p < 0.05$). After the subordinate followed the dominant's *static* gaze, the subordinate gazed towards the banana (peak at time= +17, $r = 0.2237$, $n = 578$; $-\log\text{-likelihood} = 19.9666$, $p < 0.05$).

Cross Correlation, Pair 1 *Unequal Rewards*: When the Subordinate Follows the Dominant's *Static* Gaze, Does the Subordinate Gaze Towards the Cucumber?

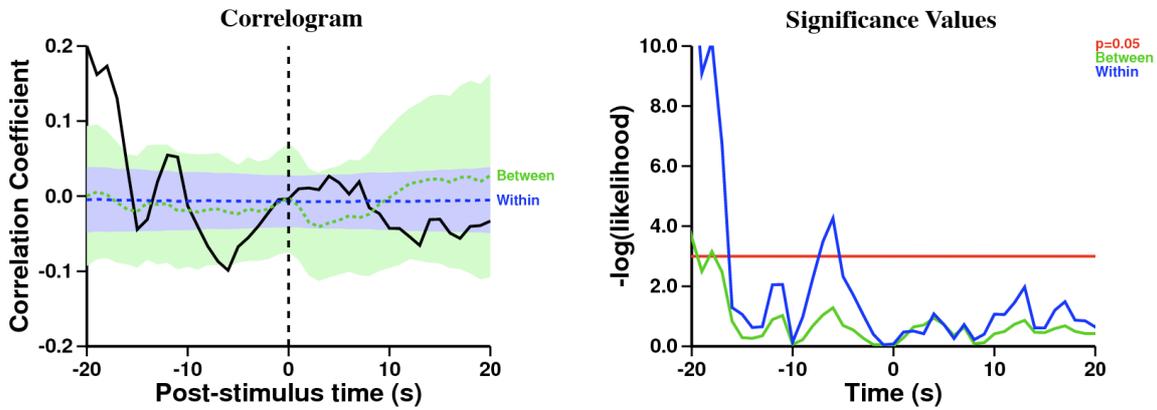


FIGURE 7.24: Referent behaviour: subordinate follows dominant's *static* gaze. Target behaviour: subordinate gazes towards cucumber. Long before the subordinate followed the dominant's *static* gaze, she gazed towards the cucumber (time= -20, $r = 0.2078$, $n = 512$; $-\log$ -likelihood= 13.4457, $p < 0.05$). Several seconds before the subordinate followed the dominant's *static* gaze, she did not gaze towards the cucumber (time= -6, $r = -0.0988$, $n = 775$; $-\log$ -likelihood= 4.2645, $p < 0.05$). Afterward there was no relationship.

V. *Unequal Rewards* analyses with dominant as referent

Cross Correlation, Pair 1 *Unequal Rewards*: When the Dominant Walks Towards the Banana, Does the Subordinate Walk Towards the Banana?

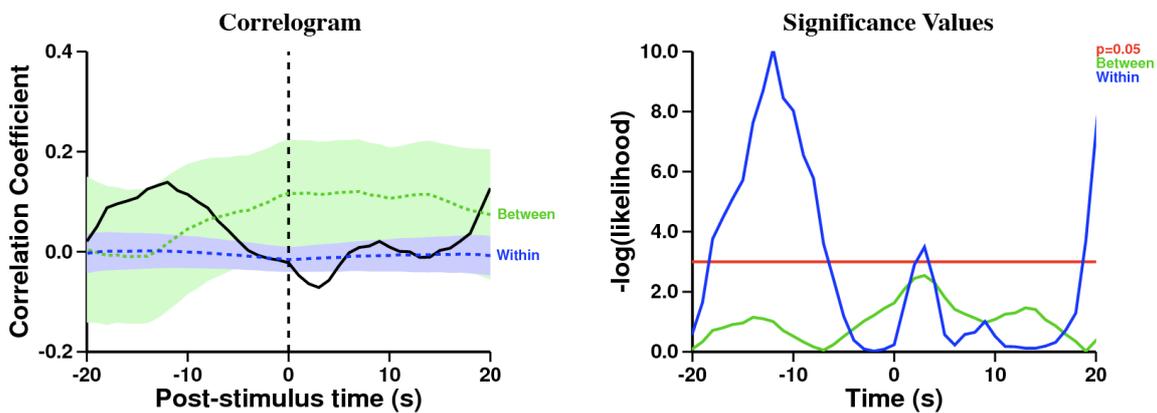


FIGURE 7.25: Referent behaviour: dominant walks towards the banana. Target behaviour: subordinate walks towards the banana. The subordinate walked towards the banana before the dominant started walking (peak at time= -12, $r = 0.1388$, $n = 666$; $-\log$ -likelihood= 10.0735, $p < 0.05$)

Cross Correlation, Pair 1 *Unequal Rewards*: When the Dominant Walks Towards the Cucumber, Does the Subordinate Walk Towards the Cucumber?

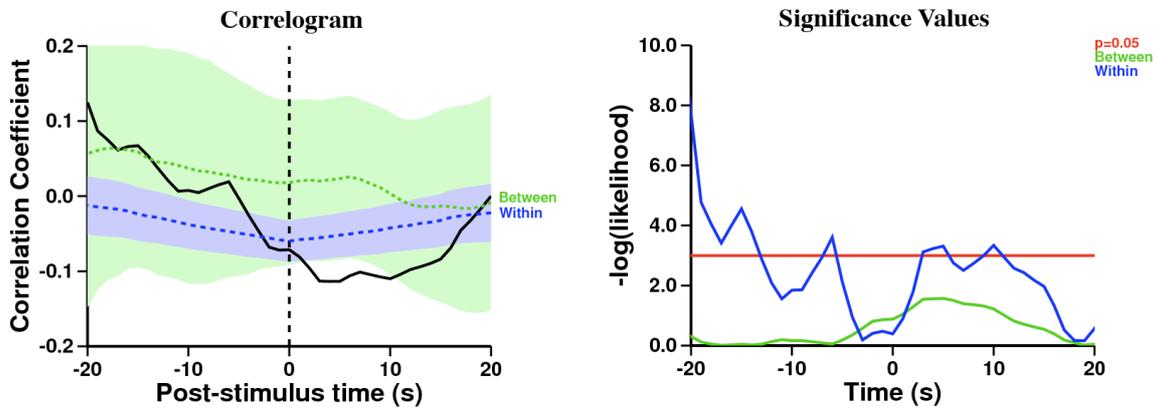


FIGURE 7.26: Referent behaviour: dominant walks towards cucumber. Target behaviour: subordinate walks towards cucumber. The subordinate walked towards the cucumber before the dominant started walking (-20, $r = 0.1249$, $n = 525$; $-\log\text{-likelihood} = 7.7333$, $p < 0.05$). After the dominant started walking towards the cucumber, the subordinate was significantly unlikely to walk towards the cucumber (peak at time = +10, $r = -0.1100$, $n = 783$; $-\log\text{-likelihood} = 3.3374$, $p < 0.05$).

Cross Correlation, Pair 1 *Unequal Rewards*: When the Dominant Gazes Towards the Banana, Does the Subordinate Gaze Towards the Banana?

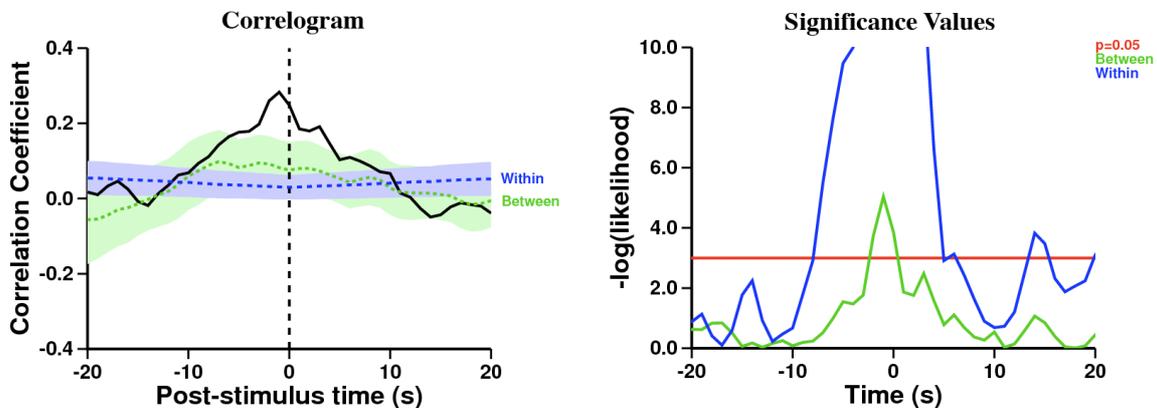


FIGURE 7.27: Referent behaviour: dominant gazes towards the banana. Target behaviour: subordinate gazes towards the banana. Before the dominant gazed towards the banana, the correlation coefficient of the subordinate gazing towards the banana is significantly more than expected from the within-trial shuffled control (peak at time = -1, $r = 0.2829$, $n = 882$; $-\log\text{-likelihood} = 29.8341$, $p < 0.05$).

Cross Correlation, Pair 1 *Unequal Rewards*: When the Dominant Gazes Towards the Cucumber, Does the Subordinate Gaze Towards the Cucumber?

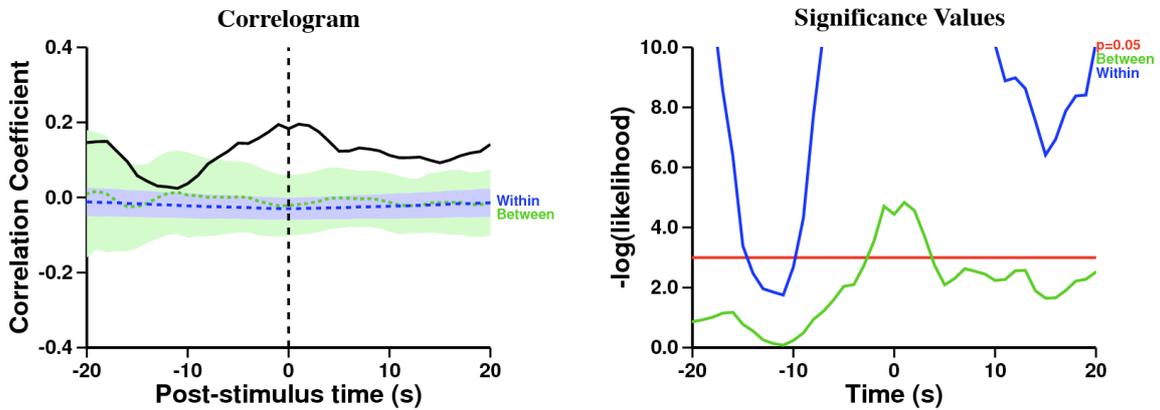


FIGURE 7.28: Referent behaviour: dominant gazes towards the cucumber. Target behaviour: subordinate gazes towards the cucumber. Before the dominant gazed towards the cucumber, the correlation coefficient of the subordinate gazing towards the cucumber is significantly more than expected from the within-trial shuffled control (peak at time= -1, $r=0.1943$, $n=882$; $-\log\text{-likelihood}=31.0918$, $p<0.05$).

Cross Correlation, Pair 1 *Unequal Rewards*: When the Dominant Walks Towards the Banana, Does the Dominant Look at the Subordinate and then Gaze Towards the Banana?

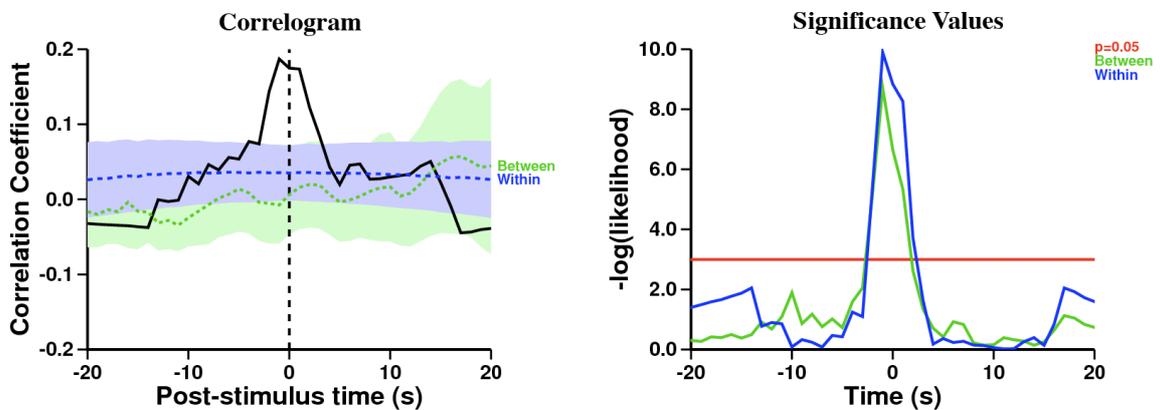


FIGURE 7.29: Referent behaviour: dominant walks towards the banana. Target behaviour: dominant looks at the subordinate and then gazes towards the banana for two seconds. Just before the dominant walked towards the banana, she alternated her gaze between the subordinate and the banana (time= -1, $r=0.1870$, $n=951$; $-\log\text{-likelihood}=9.8960$, $p<0.05$)

Cross Correlation, Pair 1 *Unequal Rewards*: When the Dominant Walks Towards the Cucumber, Does the Dominant Look at the Subordinate and then Gaze Towards the Cucumber?

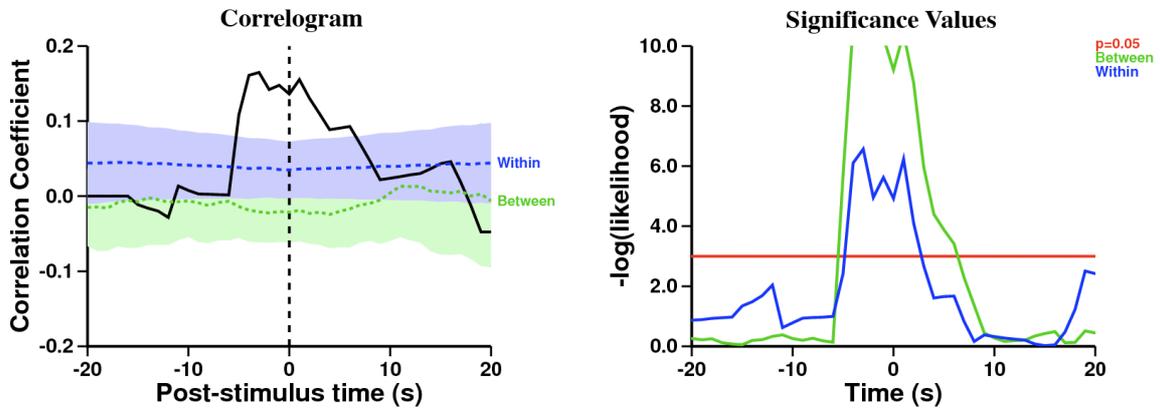


FIGURE 7.30: Referent behaviour: dominant walks towards the cucumber. Target behaviour: dominant looks at the subordinate and then gazes towards the cucumber for two seconds. Before the dominant walked towards the cucumber, she alternated gaze between the subordinate and the cucumber (time= -3, $r = 0.1648$, $n = 905$; $-\log\text{-likelihood} = 6.5676$, $p < 0.05$)

Cross Correlation, Pair 1 *Unequal Rewards*: When the Dominant Uses *Monitoring* Glances Towards the Banana, Does the Subordinate Walk Towards the Banana?

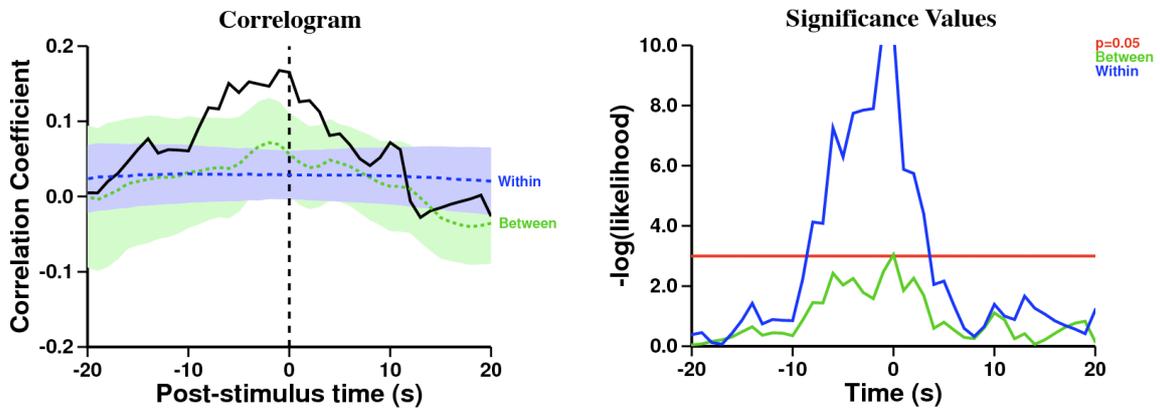


FIGURE 7.31: Referent behaviour: dominant looks at the subordinate and then gazes towards the banana for two seconds. Target behaviour: subordinate walks towards the banana. Before the dominant used *monitoring* glances, the subordinate walked towards the banana (time= -1, $r = 0.1676$, $n = 879$; $-\log\text{-likelihood} = 10.6582$, $p < 0.05$)

Cross Correlation, Pair 1 *Unequal Rewards*: When the Dominant Uses *Monitoring* Glances Towards the Cucumber, Does the Subordinate Walk Towards the Cucumber?

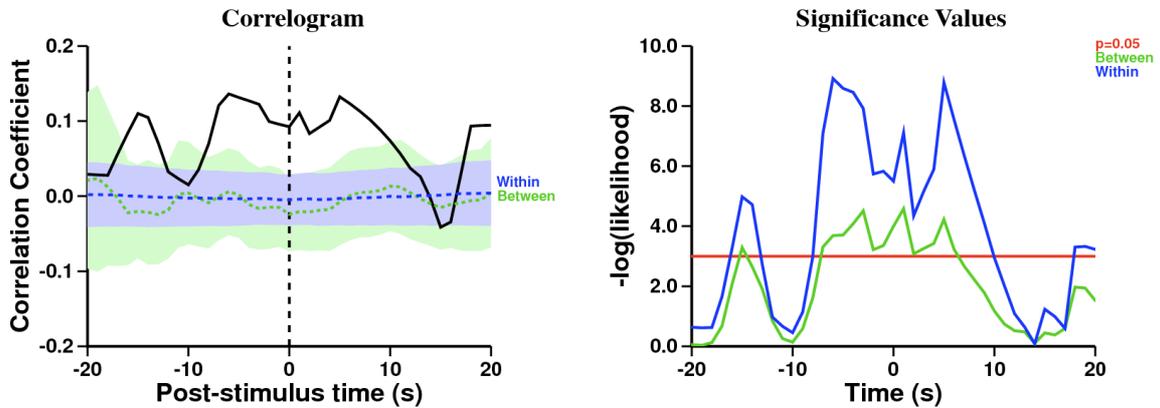


FIGURE 7.32: Referent behaviour: dominant looks at the subordinate and then gazes towards the cucumber for two seconds. Target behaviour: subordinate walks towards the cucumber. Both before and after the dominant used *monitoring* glances towards the cucumber, the subordinate walked towards the cucumber (time= -6, $r = 0.1362$, $n = 784$; $-\log$ -likelihood= 8.9196, $p < 0.05$. time= +5, $r = 0.1324$, $n = 842$; $-\log$ -likelihood= 8.7846, $p < 0.05$)

Cross Correlation, Pair 1 *Unequal Rewards*: When the Dominant Uses *Monitoring* Glances Towards the Banana, Does the Dominant Stop Walking?

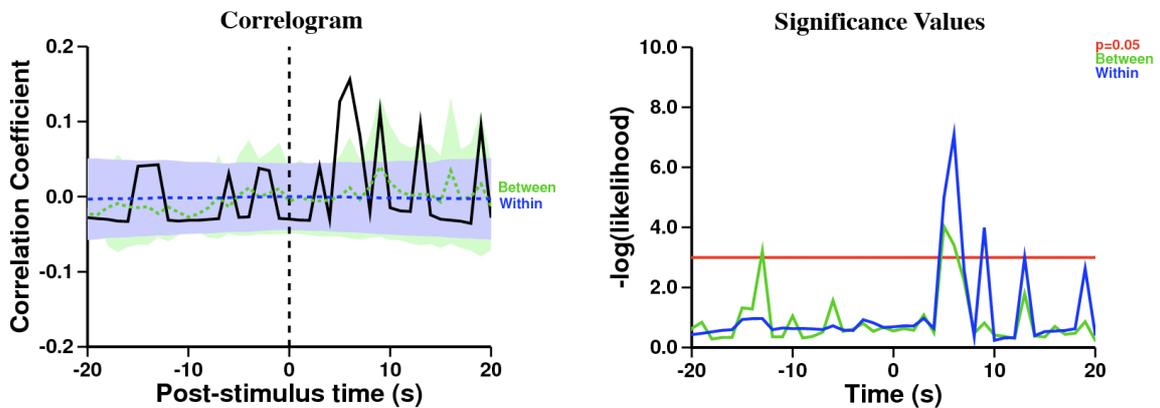


FIGURE 7.33: Referent behaviour: dominant looks at the subordinate and then gazes towards the banana for two seconds. Target behaviour: dominant stops walking. A few seconds after the dominant used *monitoring* glances towards the banana, she stopped walking for five seconds (time= +6, $r = 0.1560$, $n = 45$; $-\log$ -likelihood= 7.0852, $p < 0.05$).

Cross Correlation, Pair 1 *Unequal Rewards*: When the Dominant Uses *Monitoring* Glances Towards the Cucumber, Does the Dominant Stop Walking?

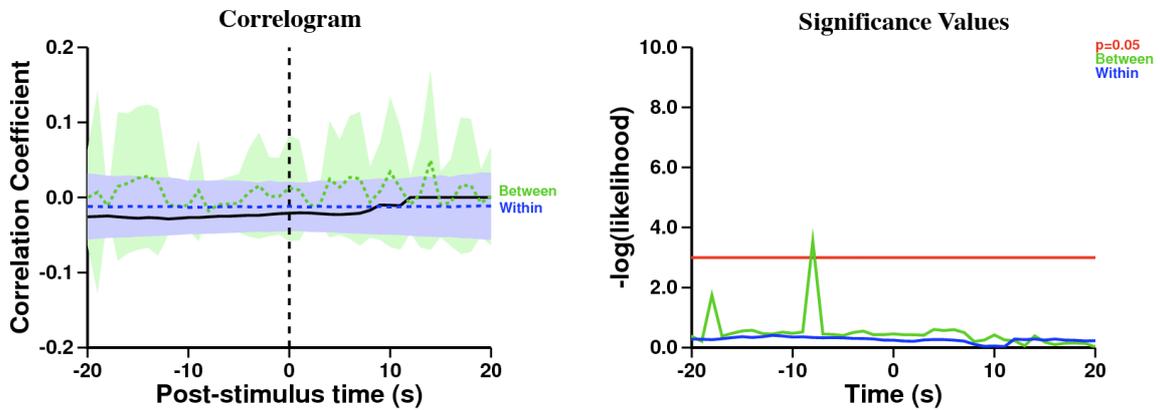


FIGURE 7.34: Referent behaviour: dominant looks at the subordinate and then gazes towards the cucumber for two seconds. Target behaviour: dominant stops walking. There is no relationship between the two variables.

Reinette & Georgia

I. Approach

Cross Correlation, Pair 2 *Unequal Rewards*: When the Subordinate Walks Towards the Banana, Does the Dominant *Approach* the Subordinate?

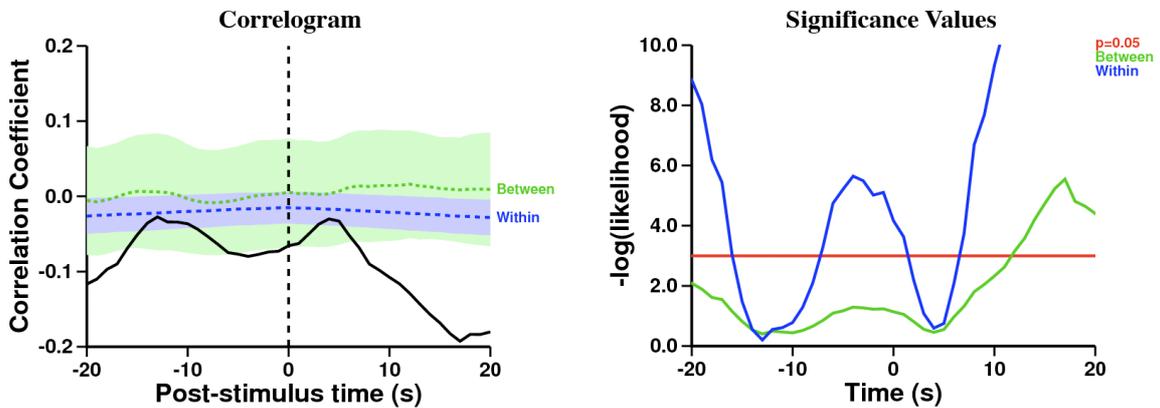


FIGURE 7.35: Referent behaviour: subordinate walks towards the banana. Target behaviour: dominant *approaches* the subordinate. Both before and after the subordinate walked towards the banana, the dominant *approached* her significantly less than expected from the within-trial shuffled control (time= -4, $r = -0.0799$, $n = 1766$; $-\log\text{-likelihood} = 5.6464$, $p < 0.05$. time= +17, $r = -0.1927$, $n = 1509$; $-\log\text{-likelihood} = 27.6489$, $p < 0.05$).

Cross Correlation, Pair 2 *Unequal Rewards*: When the Subordinate Walks Towards the Banana, Does the Subordinate Approach the Dominant?

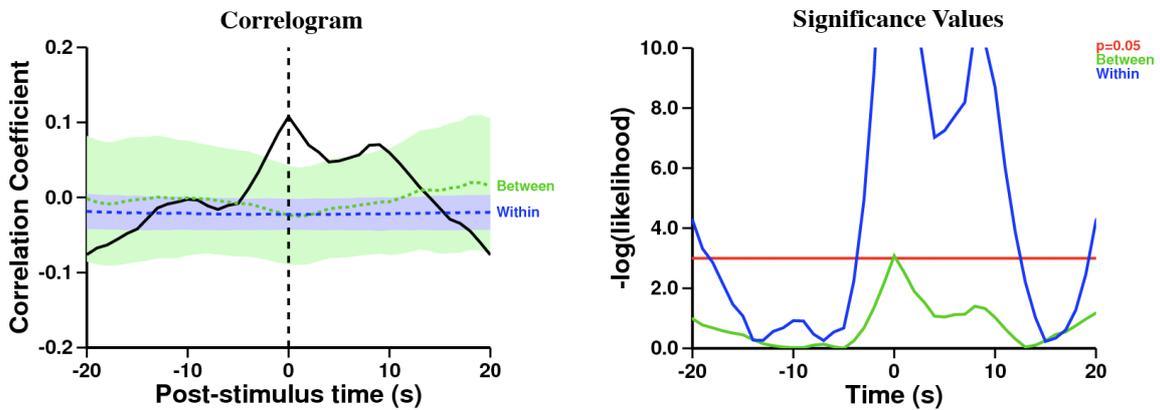


FIGURE 7.36: Referent behaviour: subordinate walks towards the banana. Target behaviour: subordinate *approaches* the dominant. At the moment that the subordinate walked towards the banana, the subordinate *approached* the dominant (time= 0, $r = 0.1075$, $n = 1838$; $-\log$ -likelihood= 21.7499, $p < 0.05$)

Cross Correlation, Pair 2 *Unequal Rewards*: When the Subordinate Walks Towards the Cucumber, Does the Dominant Approach the Subordinate?

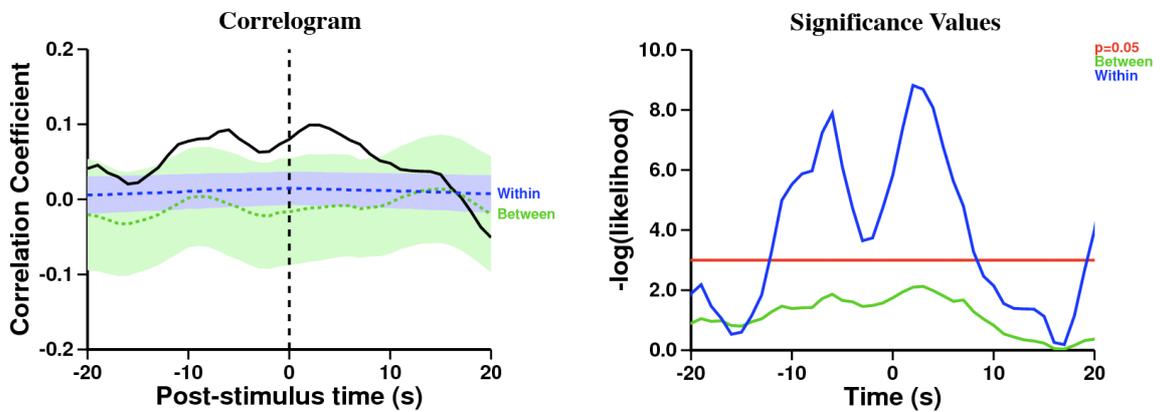


FIGURE 7.37: Referent behaviour: subordinate walks towards the cucumber. Target behaviour: dominant *approaches* the subordinate. Before and after the subordinate walked towards the cucumber, the dominant *approached* the subordinate (peak at time= +2, $r = 0.0991$, $n = 1801$; $-\log$ -likelihood= 8.8199, $p < 0.05$).

Cross Correlation, Pair 2 *Unequal Rewards*: When the Subordinate Walks Towards the Cucumber, Does the Subordinate Approach the Dominant?

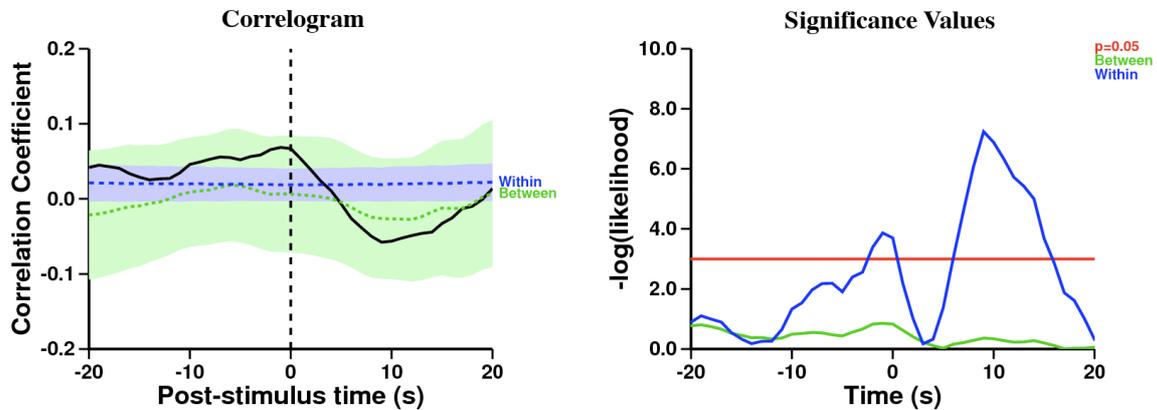


FIGURE 7.38: Referent behaviour: subordinate walks towards the cucumber. Target behaviour: subordinate *approaches* the dominant. Before the subordinate walked towards the cucumber, she *approached* the dominant (time= -1, $r = 0.0685$, $n = 1820$; $-\log\text{-likelihood} = 8.8189$, $p < 0.05$), but after the subordinate started walking towards the cucumber, she did not *approach* the dominant (time= +9, $r = -0.0577$, $n = 1663$; $-\log\text{-likelihood} = 7.2406$, $p < 0.05$).

Cross Correlation, Pair 2 *Unequal Rewards*: When the Dominant Walks Towards the Banana, Does the Dominant Approach the Subordinate?

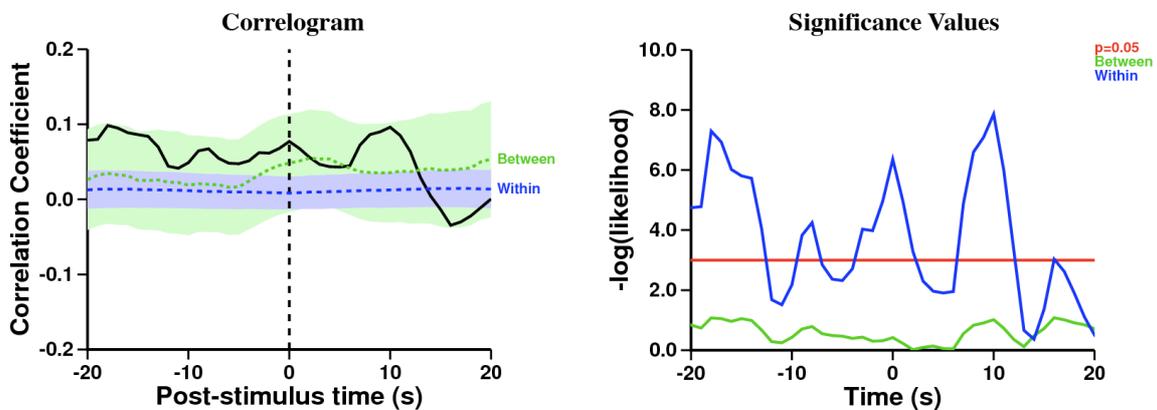


FIGURE 7.39: Referent behaviour: dominant walks towards the banana. Target behaviour: dominant *approaches* the subordinate. Many seconds before the dominant walked towards the banana, she *approached* the subordinate (time= -18, $r = 0.0984$, $n = 1490$; $-\log\text{-likelihood} = 7.2968$, $p < 0.05$). After the dominant walked towards the banana, she *approached* the subordinate (time= +10, $r = 0.0961$, $n = 1688$; $-\log\text{-likelihood} = 7.8627$, $p < 0.05$). A few seconds later, the dominant did not *approach* the subordinate (time= +16, $r = -0.0346$, $n = 1573$; $-\log\text{-likelihood} = 3.0290$, $p < 0.05$)

Cross Correlation, Pair 2 *Unequal Rewards*: When the Dominant Walks Towards the Banana, Does the Subordinate *Approach* the Dominant?

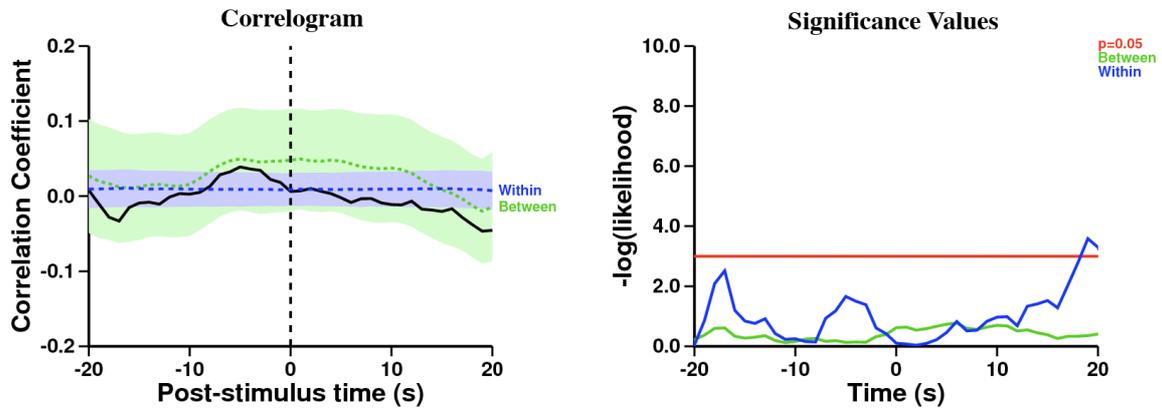


FIGURE 7.40: Referent behaviour: dominant walks towards the banana. Target behaviour: subordinate *approaches* the dominant. There is no relationship between the two variables.

Cross Correlation, Pair 2 *Unequal Rewards*: When the Dominant Walks Towards the Cucumber, Does the Dominant *Approach* the Subordinate?

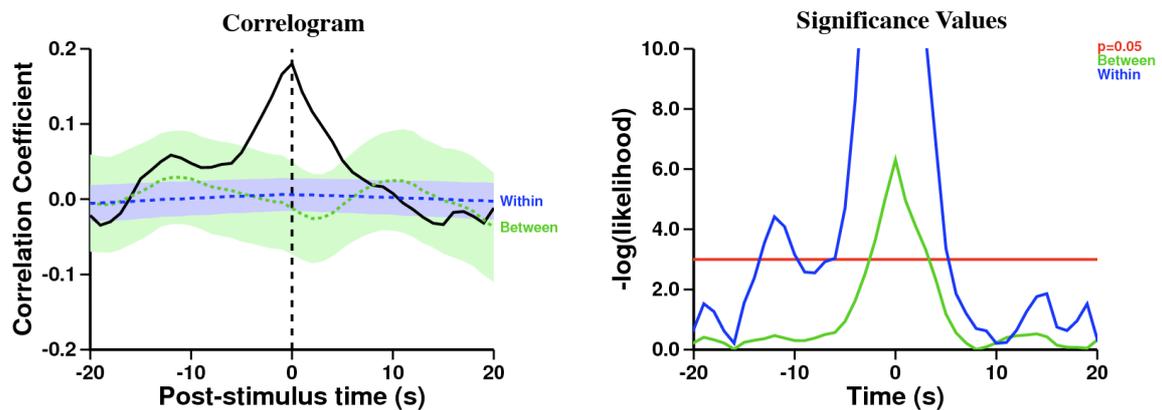


FIGURE 7.41: Referent behaviour: dominant walks towards the cucumber. Target behaviour: dominant *approaches* the subordinate. At the moment that the dominant walked towards the cucumber, she *approached* the subordinate (time= 0, $r = 0.1801$, $n = 1838$; $-\log$ -likelihood= 34.2687, $p < 0.05$)

Cross Correlation, Pair 2 *Unequal Rewards*: When the Dominant Walks Towards the Cucumber, Does the Subordinate *Approach* the Dominant?

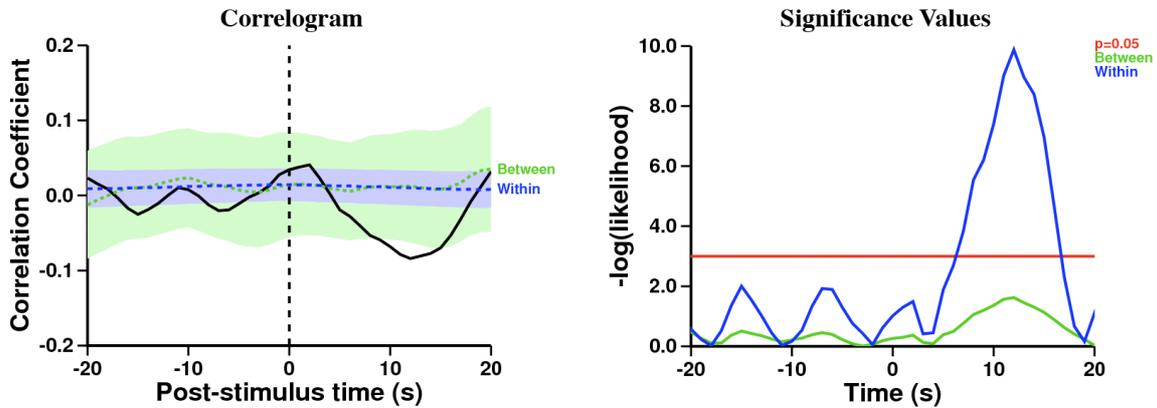


FIGURE 7.42: Referent behaviour: dominant walks towards the cucumber. Target behaviour: subordinate *approaches* the dominant. Several seconds after the dominant walked towards the cucumber, the subordinate was significantly unlikely to *approach* the dominant (time= +12, $r = -0.0841$, $n = 1649$; $-\log\text{-likelihood} = 9.8778$, $p < 0.05$)

II. Footsteps

Cross Correlation, Pair 2 *Unequal Rewards*: When the Subordinate Walks Towards the Banana, Does the Dominant Follow in the Subordinate's Footsteps?

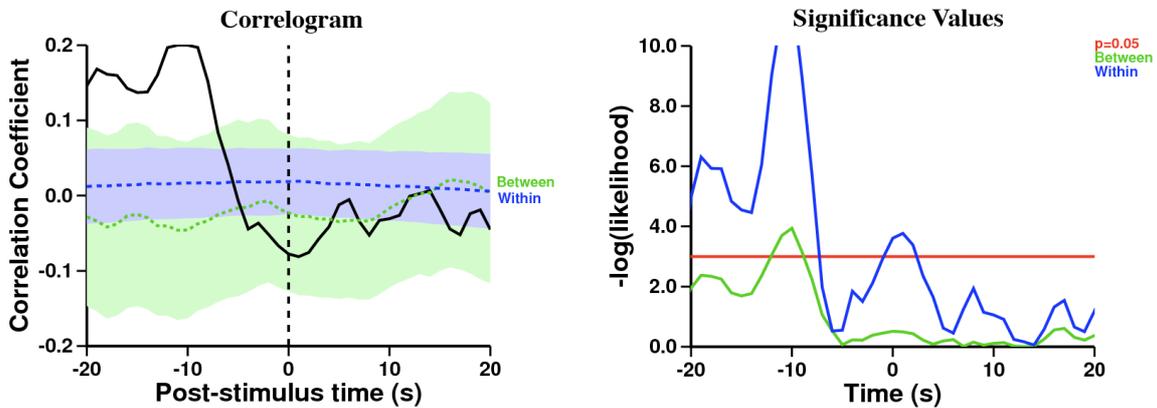


FIGURE 7.43: Referent behaviour: subordinate walks towards the banana. Target behaviour: dominant follows in the subordinate's *footsteps*. After the subordinate walked towards the banana, the dominant did not follow in her *footsteps* (time= +1, $r = -0.0812$, $n = 462$; $-\log\text{-likelihood} = 3.7683$, $p < 0.05$). Several seconds before the subordinate walked towards the banana, the dominant followed in her footsteps significantly more than expected from the within-trial shuffled control (time= -10, $r = 0.2293$, $n = 410$; $-\log\text{-likelihood} = 11.8148$, $p < 0.05$)

Cross Correlation, Pair 2 *Unequal Rewards*: When the Subordinate Walks Towards the Banana, Does the Subordinate Follow in the Dominant's *Footsteps*?

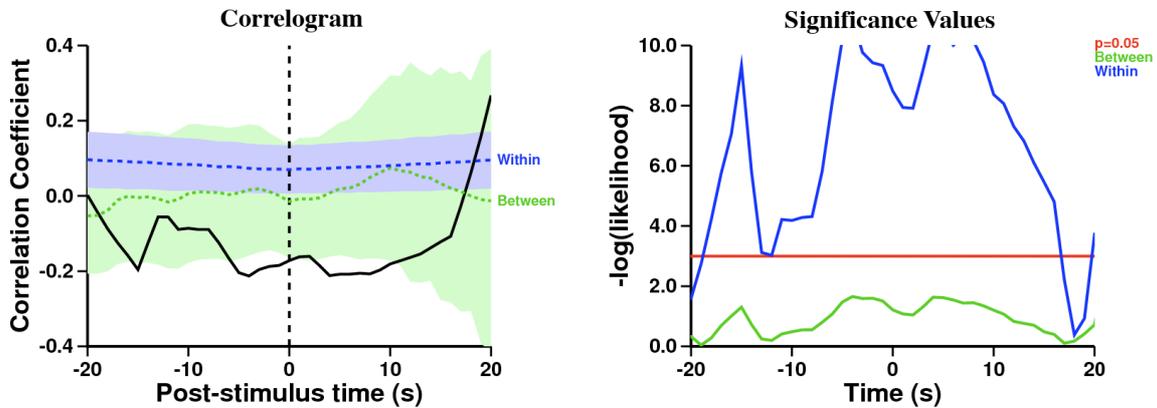


FIGURE 7.44: Referent behaviour: subordinate walks towards the banana. Target behaviour: subordinate walks in dominant's *footsteps*. Before and after the subordinate walked towards the banana, she did not follow in the dominant's *footsteps* (peak at time= +4, $r = -0.2120$, $n = 198$; $-\log\text{-likelihood} = 10.5566$, $p < 0.05$)

Cross Correlation, Pair 2 *Unequal Rewards*: When the Subordinate Walks Towards the Cucumber, Does the Dominant Follow in the Subordinate's *Footsteps*?

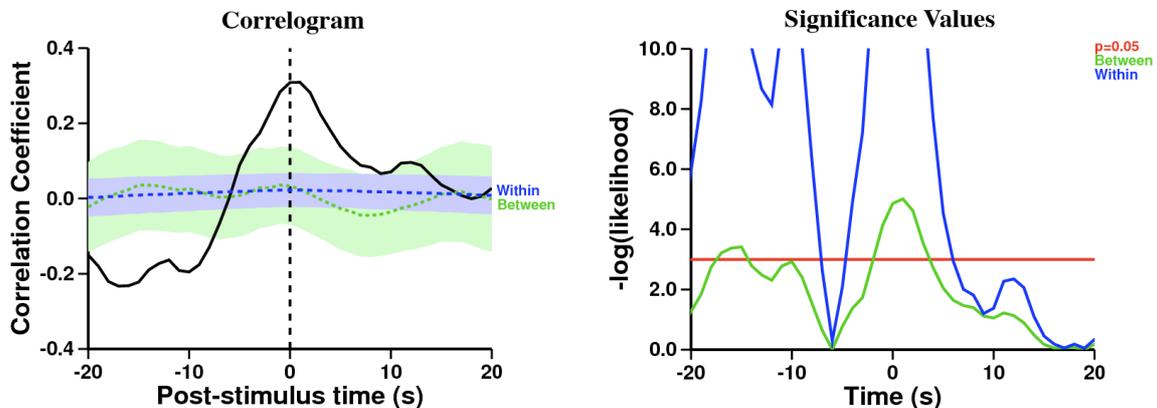


FIGURE 7.45: Referent behaviour: subordinate walks towards cucumber. Target behaviour: dominant walks in subordinate's *footsteps*. Before the subordinate walked towards the cucumber, the dominant did not follow in her *footsteps* (time= -16, $r = -0.2319$, $n = 391$; $-\log\text{-likelihood} = 13.3773$, $p < 0.05$). At the moment that the subordinate walked towards the cucumber, the dominant followed in her *footsteps* significantly more than expected from the within-trial shuffled control (time= 0, $r = 0.3085$, $n = 463$; $-\log\text{-likelihood} = 22.0080$, $p < 0.05$)

Cross Correlation, Pair 2 *Unequal Rewards*: When the Subordinate Walks Towards the Cucumber, Does the Subordinate Follow in the Dominant's *Footsteps*?

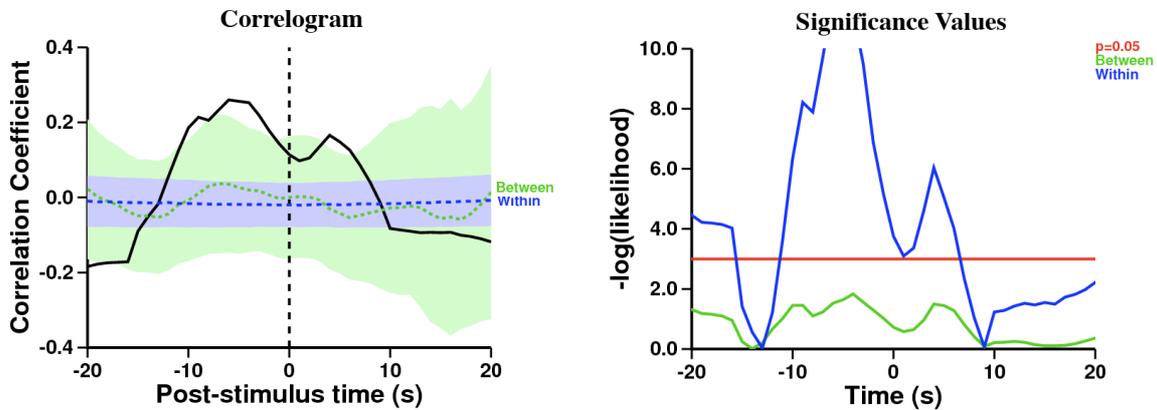


FIGURE 7.46: Referent behaviour: subordinate walks towards cucumber. Target behaviour: subordinate walks in dominant's *footsteps*. Before and after the subordinate walked towards the cucumber, she followed in the dominant's *footsteps* (time= -6, $r = 0.2598$, $n = 224$; $-\log$ -likelihood= 11.7491, $p < 0.05$. time= +4, $r = 0.1657$, $n = 198$; $-\log$ -likelihood= 6.0358, $p < 0.05$)

Cross Correlation, Pair 2 *Unequal Rewards*: When the Dominant Walks Towards the Banana, Does the Dominant Follow in the Subordinate's *Footsteps*?

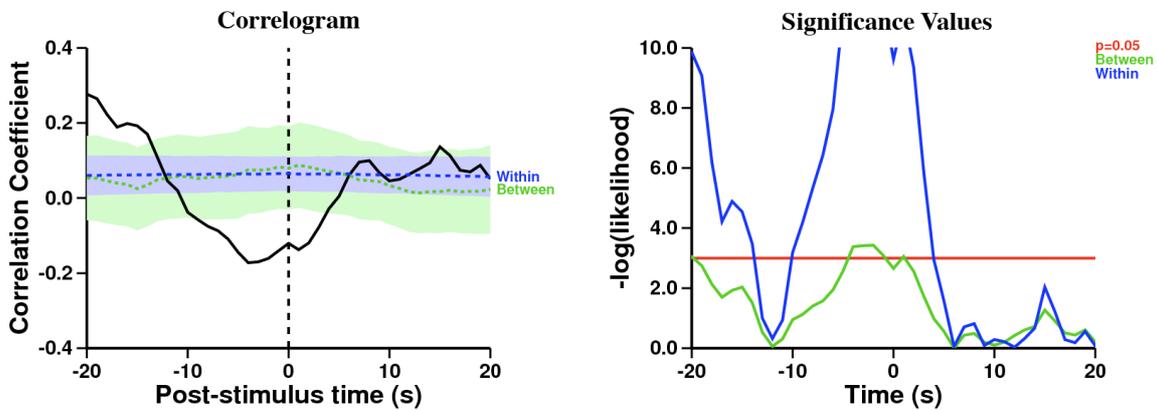


FIGURE 7.47: Referent behaviour: dominant walks towards banana. Target behaviour: dominant walks in subordinate's *footsteps*. Long before the dominant walked towards the banana, she walked in the subordinate's *footsteps* (time= -2, $r = 0.2768$, $n = 374$; $-\log$ -likelihood= 9.8578, $p < 0.05$). a few seconds before the dominant walked towards the banana, she did not walk in the subordinate's *footsteps* (time= -4, $r = -0.1723$, $n = 445$; $-\log$ -likelihood= 14.1409, $p < 0.05$). Afterward there was no relationship.

Cross Correlation, Pair 2 *Unequal Rewards*: When the Dominant Walks Towards the Banana, Does the Subordinate Follow in the Dominant's *Footsteps*?

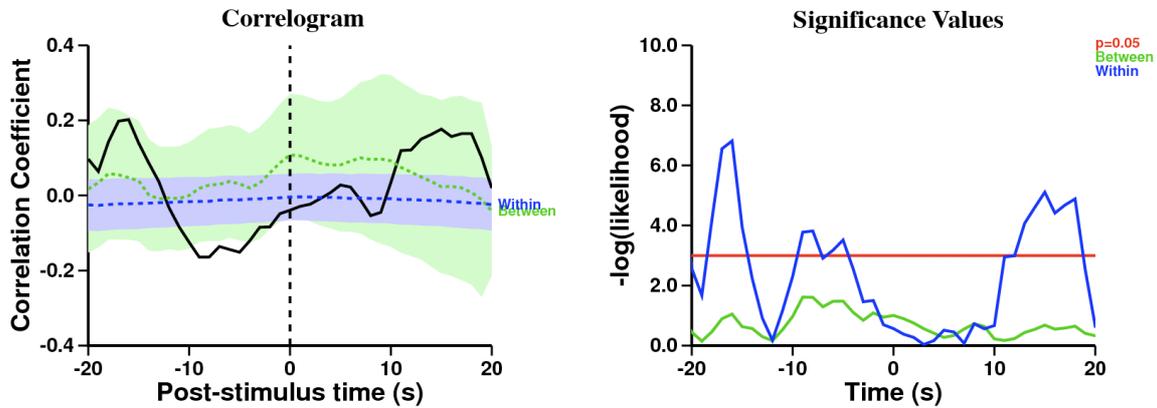


FIGURE 7.48: Referent behaviour: dominant walks towards banana. Target behaviour: subordinate walks in dominant's *footsteps*. Several seconds before the dominant walked towards the banana, the subordinate walked in her *footsteps* (time= -16, $r = 0.2021$, $n = 194$; $-\log\text{-likelihood} = 6.8152$, $p < 0.05$). A few seconds before the dominant walked towards the banana, the subordinate did not walk in her *footsteps* (time= -8, $r = -0.1641$, $n = 212$; $-\log\text{-likelihood} = 3.8165$, $p < 0.05$). Many seconds after the dominant walked towards the banana, the subordinate did follow in her *footsteps* (time= +15, $r = 0.1767$, $n = 171$; $-\log\text{-likelihood} = 5.1094$, $p < 0.05$)

Cross Correlation, Pair 2 *Unequal Rewards*: When the Dominant Walks Towards the Cucumber, Does the Dominant Follow in the Subordinate's *Footsteps*?

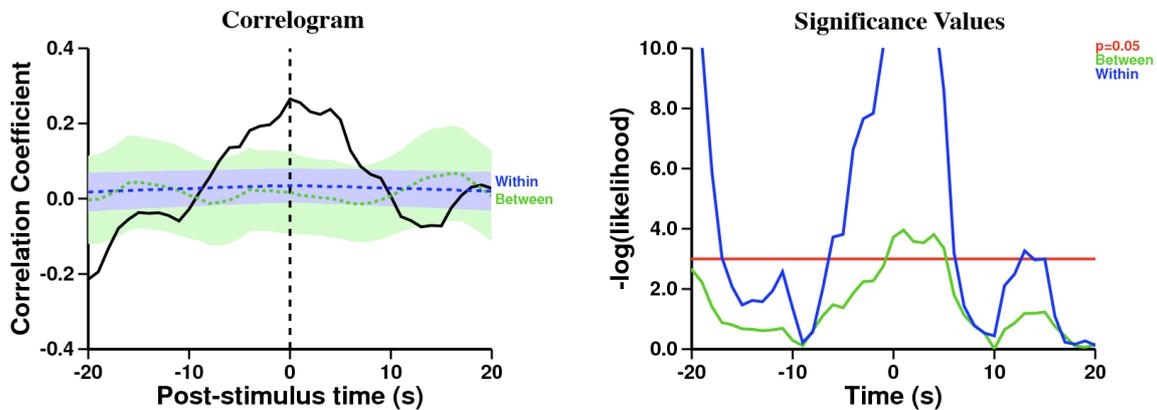


FIGURE 7.49: Referent behaviour: dominant walks towards cucumber. Target behaviour: dominant walks in subordinate's *footsteps*. At the moment that the dominant walked towards the cucumber, she was walking in the subordinate's *footsteps* (time= 0, $r = 0.2650$, $n = 463$; $-\log\text{-likelihood} = 14.6848$, $p < 0.05$). Both before and after, the dominant was significantly unlikely to follow in the subordinate's *footsteps* (time= -20, $r = -0.2146$, $n = 374$; $-\log\text{-likelihood} = 11.6636$, $p < 0.05$. time= +13, $r = -0.0750$, $n = 417$; $-\log\text{-likelihood} = 3.2667$, $p < 0.05$).

Cross Correlation, Pair 2 *Unequal Rewards*: When the Dominant Walks Towards the Cucumber, Does the Subordinate Follow in the Dominant's *Footsteps*?

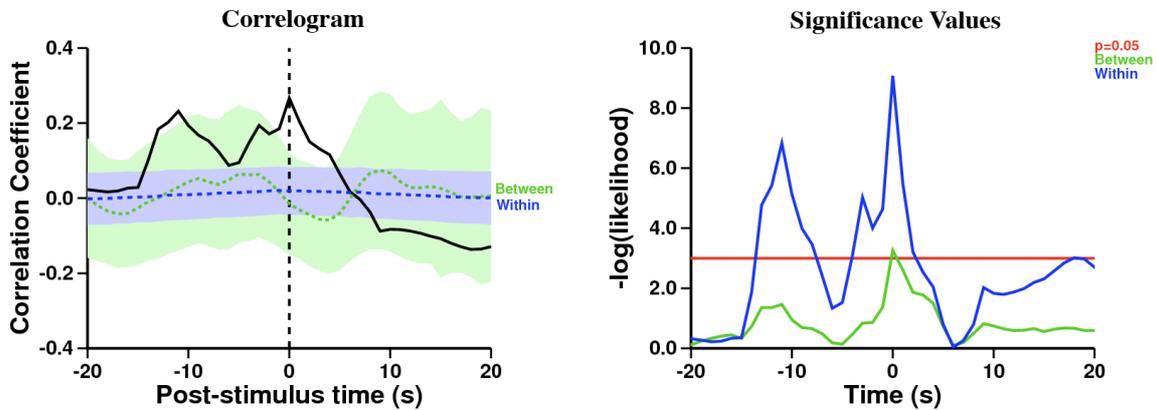


FIGURE 7.50: Referent behaviour: dominant walks towards cucumber. Target behaviour: subordinate walks in dominant's *footsteps*. Before, and at the moment that the dominant walked towards the cucumber, the subordinate walked in her *footsteps* (time= -11, $r= 0.2316$, $n= 202$; $-\log\text{-likelihood}= 6.8316$, $p<0.05$. time= 0, $r= 0.2667$, $n= 233$; $-\log\text{-likelihood}= 9.0772$, $p<0.05$). Many seconds after the dominant walked towards the cucumber, the subordinate did not walk in her *footsteps* (time= +18, $r= -0.1366$, $n= 165$; $-\log\text{-likelihood}= 3.0145$, $p<0.05$)

III. Convergence

Cross Correlation, Pair 2 *Unequal Rewards*: When the Subordinate Walks Towards the Banana, Do Both Chimpanzees Converge?

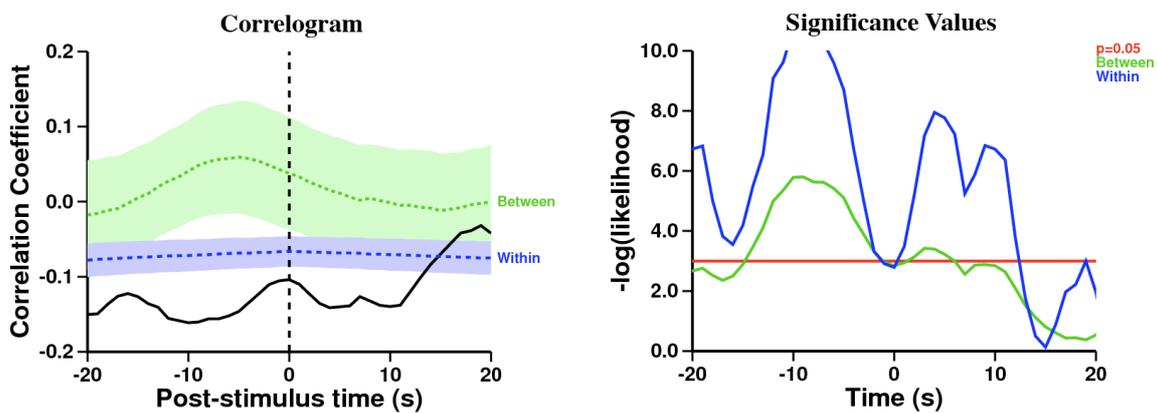


FIGURE 7.51: Referent behaviour: subordinate walks towards banana. Target behaviour: both chimpanzees *converge*. Both before and after the subordinate walked towards the banana, the chimpanzees *converged* significantly less than expected from the within-trial shuffled control (time= -10, $r= -0.1613$, $n= 1653$; $-\log\text{-likelihood}= 10.7514$, $p<0.05$. time= +4, $r= -0.1413$, $n= 1763$; $-\log\text{-likelihood}= 7.9512$, $p<0.05$).

Cross Correlation, Pair 2 *Unequal Rewards*: When the Subordinate Walks Towards the Cucumber, Do Both Chimpanzees Converge?

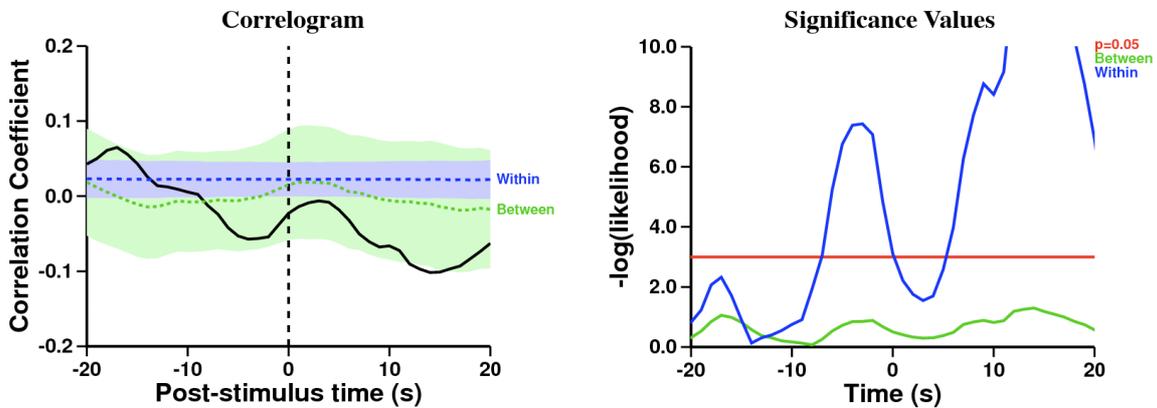


FIGURE 7.52: Referent behaviour: subordinate walks towards cucumber. Target behaviour: both chimpanzees *converge*. Before and after the subordinate walked towards the cucumber, the chimpanzees *converged* significantly less than expected from the within-trial shuffled control (time= -3, $r = -0.0564$, $n = 1784$; $-\log\text{-likelihood} = 7.4306$, $p < 0.05$. time= +14, $r = -0.1017$, $n = 1564$; $-\log\text{-likelihood} = 14.1627$, $p < 0.05$).

Cross Correlation, Pair 2 *Unequal Rewards*: When the Dominant Walks Towards the Banana, Do Both Chimpanzees Converge?

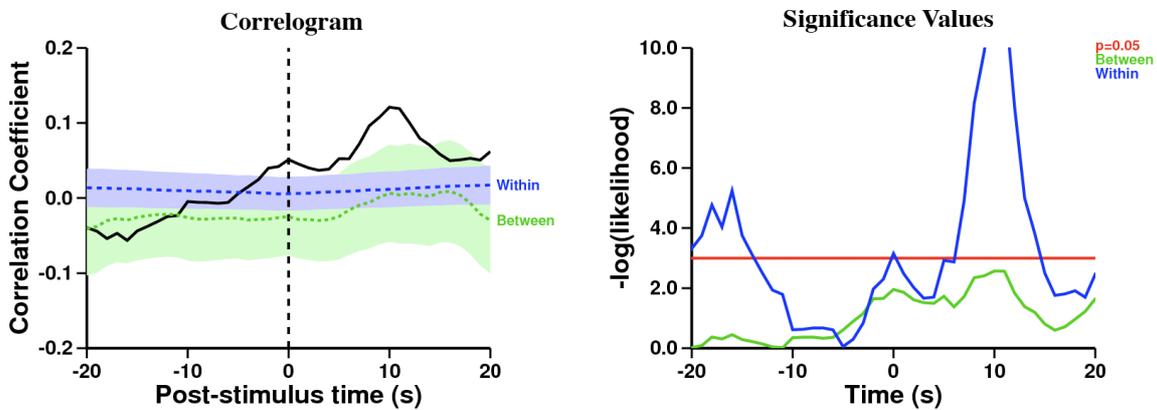


FIGURE 7.53: Referent behaviour: dominant walks towards banana. Target behaviour: both chimpanzees *converge*. After the dominant walked towards the banana, both chimpanzees *converged* (time= +10, $r = 0.1210$, $n = 1688$; $-\log\text{-likelihood} = 12.2866$, $p < 0.05$). Before the dominant walked towards the banana, the chimpanzees were significantly unlikely to *converge* (time= -16, $r = -0.0564$, $n = 1524$; $-\log\text{-likelihood} = 5.2440$, $p < 0.05$)

Cross Correlation, Pair 2 *Unequal Rewards*: When the Dominant Walks Towards the Cucumber, Do Both Chimpanzees Converge?

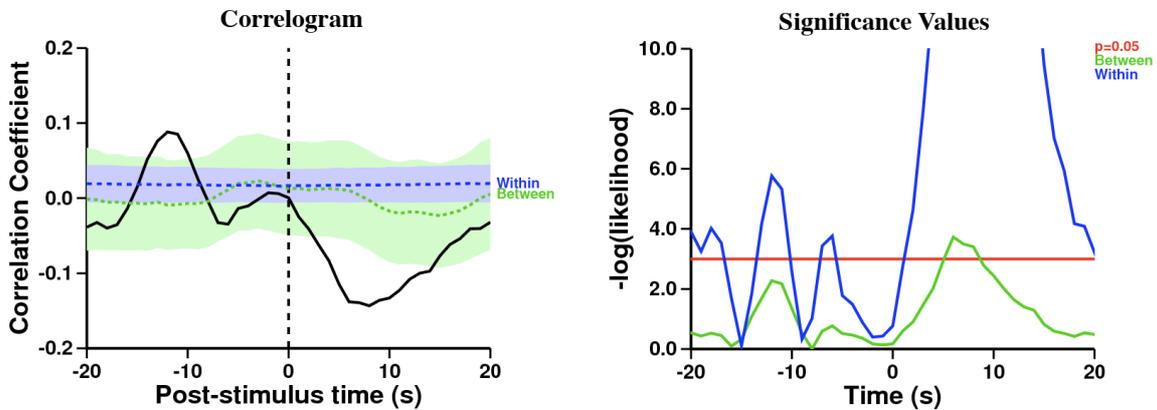


FIGURE 7.54: Referent behaviour: dominant walks towards cucumber. Target behaviour: both chimpanzees *converge*. Before the dominant walked towards the cucumber, the chimpanzees did *converge* (time= -12, $r = 0.0882$, $n = 1598$; $-\log\text{-likelihood} = 5.7634$, $p < 0.05$). Shortly before, and after the dominant started walking towards the cucumber, the chimpanzees did not *converge* (time= -6, $r = -0.0347$, $n = 1717$; $-\log\text{-likelihood} = 3.7630$, $p < 0.05$. time= +8, $r = -0.1434$, $n = 1728$; $-\log\text{-likelihood} = 26.1261$, $p < 0.05$).

IV. *Static Gaze*

Cross Correlation, Pair 2 *Unequal Rewards*: When the Dominant Follows the Subordinate's *Static Gaze*, Does the Dominant Gaze Towards the Banana?

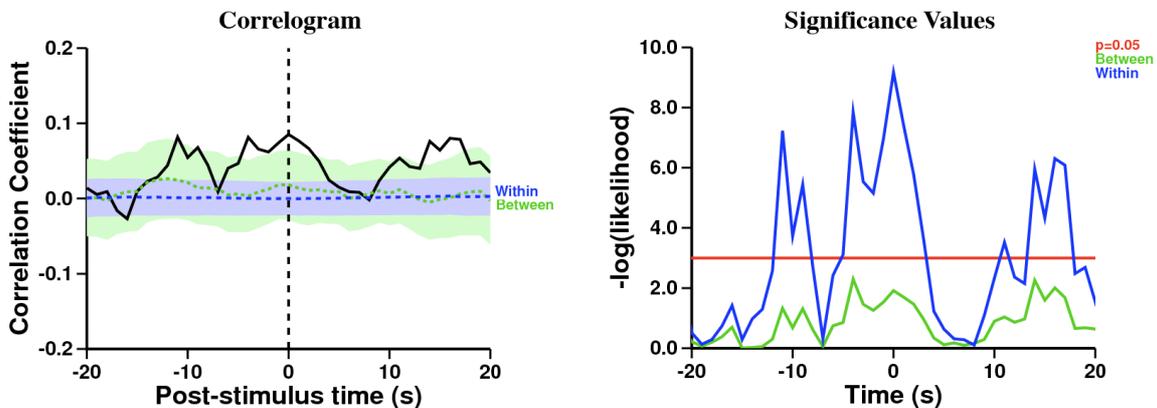


FIGURE 7.55: Referent behaviour: dominant follows subordinate's *static gaze*. Target behaviour: dominant gazes towards banana. Before, at the moment, and after the dominant followed the subordinate's *static gaze*, the dominant gazed towards the banana (time= -11, $r = 0.0817$, $n = 1692$; $-\log\text{-likelihood} = 7.2307$, $p < 0.05$. time= 0, $r = 0.0852$, $n = 1840$; $-\log\text{-likelihood} = 9.1746$, $p < 0.05$. time= +16, $r = 0.0801$, $n = 1538$; $-\log\text{-likelihood} = 6.3034$, $p < 0.05$).

Cross Correlation, Pair 2 *Unequal Rewards*: When the Dominant Follows the Subordinate's *Static* Gaze, Does the Dominant Gaze Towards the Cucumber?

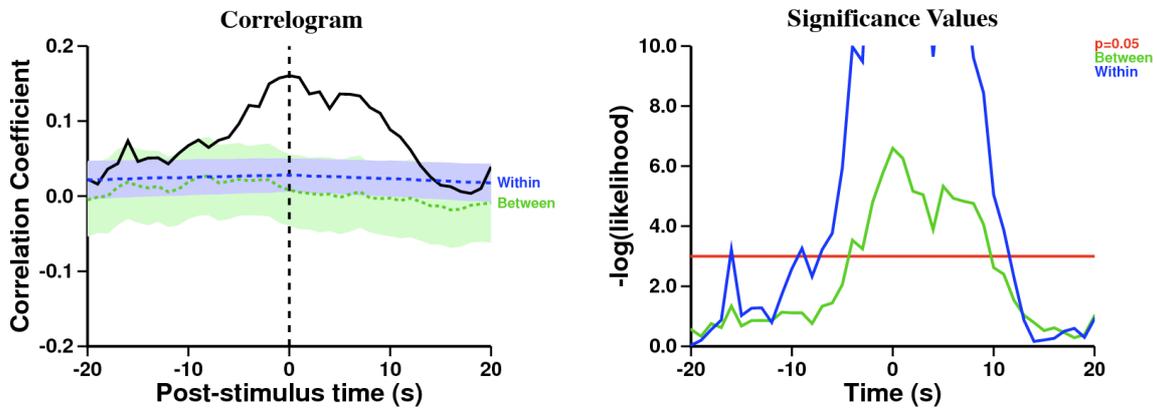


FIGURE 7.56: Referent behaviour: dominant follows subordinate's *static* gaze. Target behaviour: dominant gazes towards cucumber. At the moment the dominant followed the subordinate's *static* gaze, the dominant gazed towards the cucumber (time= 0, $r= 0.1605$, $n= 1840$; $-\log\text{-likelihood}= 19.6971$, $p<0.05$).

Cross Correlation, Pair 2 *Unequal Rewards*: When the Dominant Follows the Subordinate's *Static* Gaze, Does the Subordinate Gaze Towards the Banana?

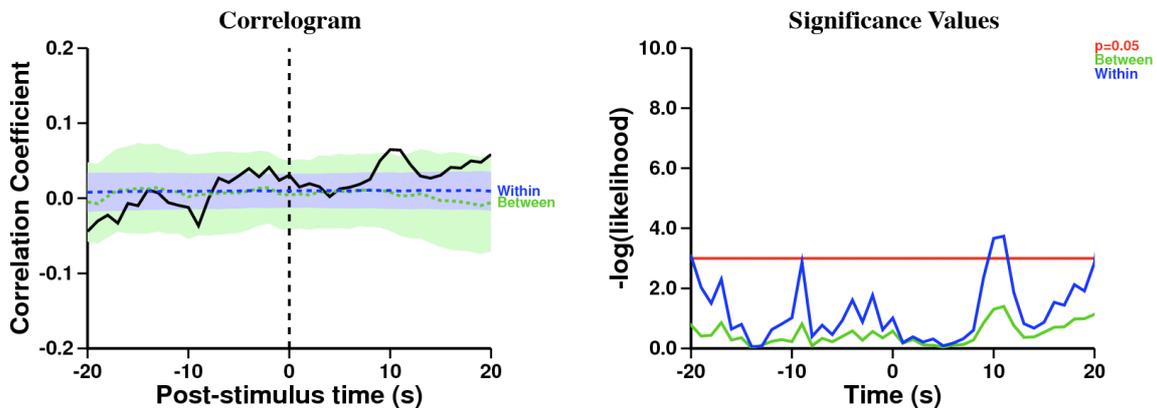


FIGURE 7.57: Referent behaviour: dominant follows subordinate's *static* gaze. Target behaviour: subordinate gazes towards banana. Before the dominant followed the subordinate's *static* gaze, the subordinate did not gaze towards the banana (time= -9, $r= -0.0367$, $n= 1634$; $-\log\text{-likelihood}= 2.8732$, ns). Several seconds after the dominant followed the subordinate's *static* gaze, the subordinate gazed towards the banana (time= +11, $r= 0.0642$, $n= 1634$; $-\log\text{-likelihood}= 3.7353$, $p<0.05$).

Cross Correlation, Pair 2 *Unequal Rewards*: When the Dominant Follows the Subordinate's *Static* Gaze, Does the Subordinate Gaze Towards the Cucumber?

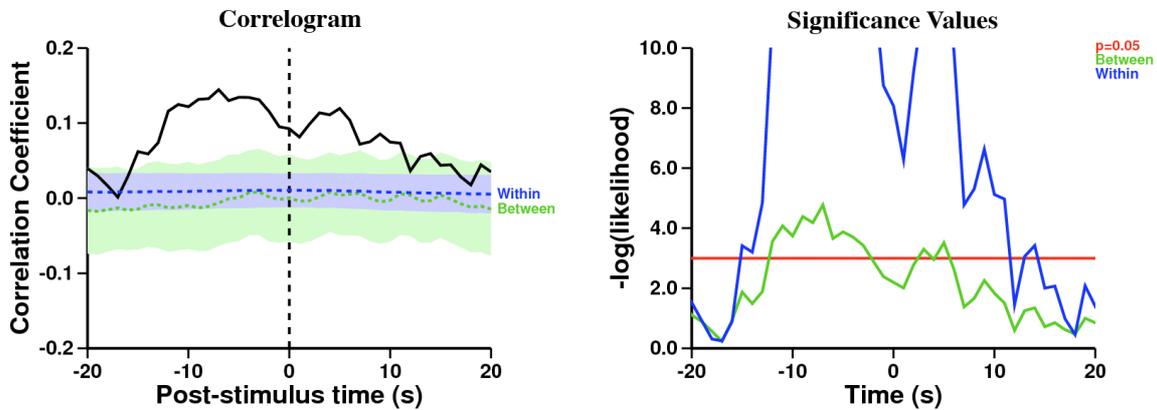


FIGURE 7.58: Referent behaviour: dominant follows subordinate's *static* gaze. Target behaviour: subordinate gazes towards cucumber. Before and after the dominant followed the subordinate's *static* gaze, the subordinate gazed towards the cucumber (time= -7, $r = 0.1445$, $n = 1719$; $-\log\text{-likelihood} = 18.7198$, $p < 0.05$. time= +5, $r = -.1195$, $n = 1749$; $-\log\text{-likelihood} = 12.9009$, $p < 0.05$).

Cross Correlation, Pair 2 *Unequal Rewards*: When the Subordinate Follows the Dominant's *Static* Gaze, Does the Dominant Gaze Towards the Banana?

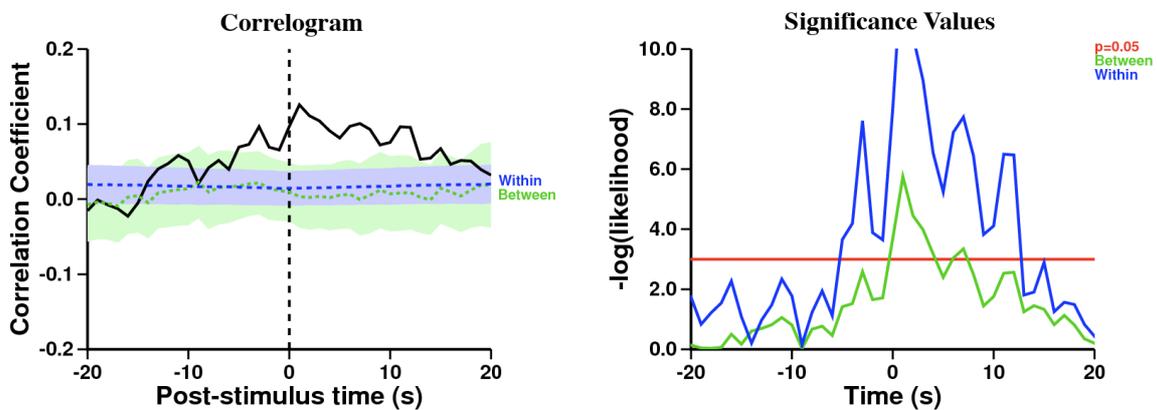


FIGURE 7.59: Referent behaviour: subordinate follows dominant's *static* gaze. Target behaviour: dominant gazes towards banana. Before and after the subordinate followed the dominant's *static* gaze, the dominant gazed towards the banana (peak at time= +1, $r = 0.1257$, $n = 1832$; $-\log\text{-likelihood} = 13.2206$, $p < 0.05$)

Cross Correlation, Pair 2 *Unequal Rewards*: When the Subordinate Follows the Dominant's *Static* Gaze, Does the Dominant Gaze Towards the Cucumber?

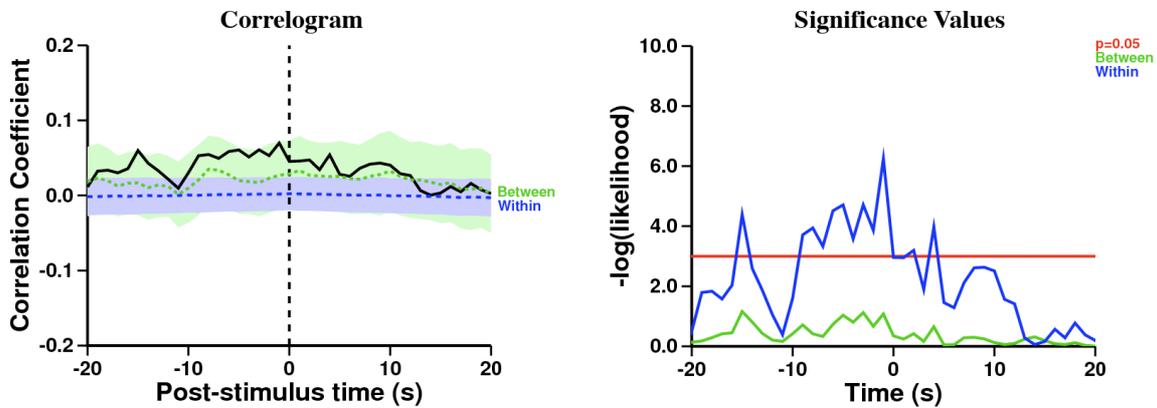


FIGURE 7.60: Referent behaviour: subordinate follows dominant's *static* gaze. Target behaviour: dominant gazes towards cucumber. Before and after the subordinate followed the dominant's *static* gaze, the dominant gazed towards the cucumber (peak at time= -1, $r=0.0698$, $n=1848$; $-\log\text{-likelihood}=6.2494$, $p<0.05$)

Cross Correlation, Pair 2 *Unequal Rewards*: When the Subordinate Follows the Dominant's *Static* Gaze, Does the Subordinate Gaze Towards the Banana?

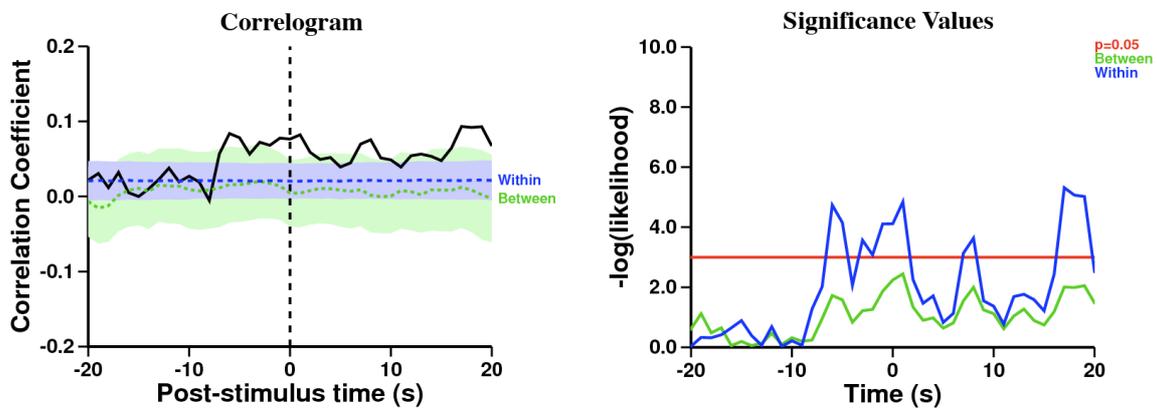


FIGURE 7.61: Referent behaviour: subordinate follows dominant's *static* gaze. Target behaviour: subordinate gazes towards banana. Before and after the subordinate followed the dominant's *static* gaze, the subordinate gazed towards the banana (time= -6, $r=0.0838$, $n=1740$; $-\log\text{-likelihood}=4.7352$, $p<0.05$. time= +1, $r=0.0821$, $n=1832$; $-\log\text{-likelihood}=4.8416$, $p<0.05$)

Cross Correlation, Pair 2 *Unequal Rewards*: When the Subordinate Follows the Dominant's *Static* Gaze, Does the Subordinate Gaze Towards the Cucumber?

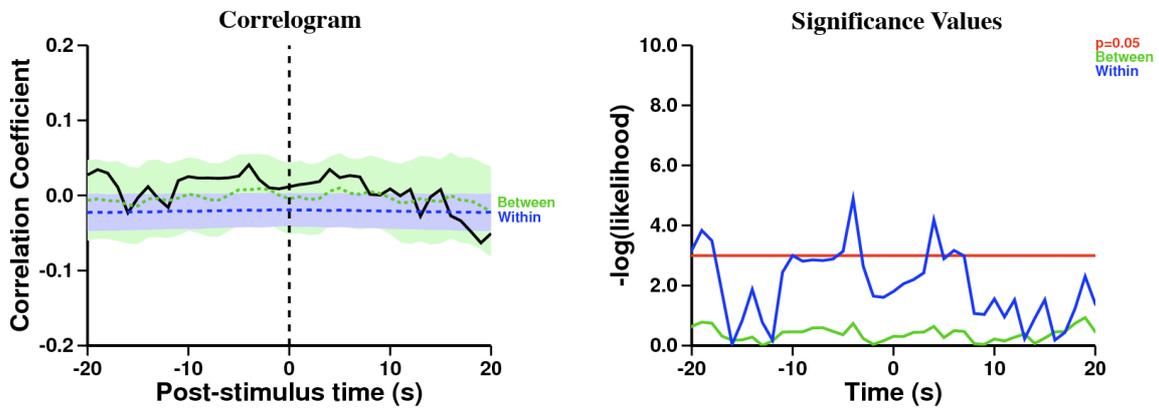


FIGURE 7.56: Referent behaviour: subordinate follows dominant's *static* gaze. Target behaviour: subordinate gazes towards cucumber. Before and after the subordinate followed the dominant's *static* gaze, the subordinate gazed towards the cucumber (time= -4, $r = 0.0409$, $n = 1778$; $-\log\text{-likelihood} = 4.8932$, $p < 0.05$. time= +4, $r = 0.0345$, $n = 1772$; $-\log\text{-likelihood} = 4.1897$, $p < 0.05$).

V. *Unequal Rewards* analyses with the dominant as referent

Cross Correlation, Pair 2 *Unequal Rewards*: When the Dominant Walks Towards the Banana, Does the Subordinate Walk Towards the Banana?

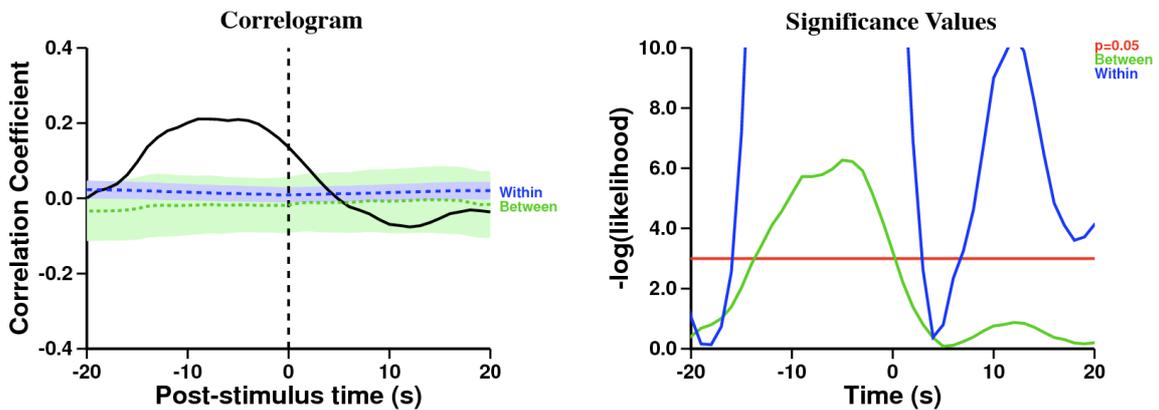


FIGURE 7.57: Referent behaviour: dominant walks towards banana. Target behaviour: subordinate walks towards banana. The subordinate walked towards the banana before the dominant (peak at time= -4, $r = 0.2066$, $n = 1763$; $-\log\text{-likelihood} = 45.7881$, $p < 0.05$). After the dominant started walking towards the banana, the subordinate was significantly unlikely to walk towards the banana (peak at time= +12, $r = -0.0761$, $n = 1665$; $-\log\text{-likelihood} = 10.4127$, $p < 0.05$).

Cross Correlation, Pair 2 *Unequal Rewards*: When the Dominant Walks Towards the Cucumber, Does the Subordinate Walk Towards the Cucumber?

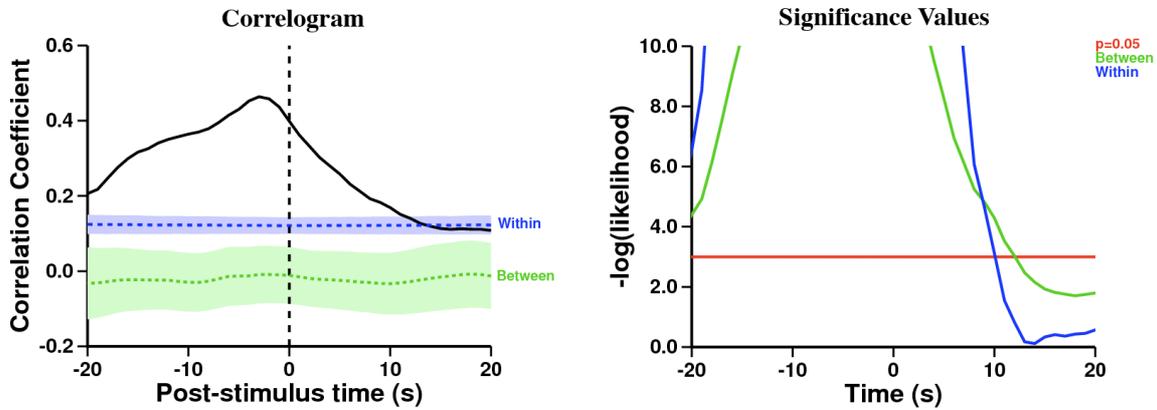


FIGURE 7.58: Referent behaviour: dominant walks towards cucumber. Target behaviour: subordinate walks towards cucumber. The subordinate walked towards the cucumber before the dominant (peak at time= -3, $r = 0.4637$, $n = 1782$; $-\log\text{-likelihood} = 110.6573$, $p < 0.05$).

Cross Correlation, Pair 2 *Unequal Rewards*: When the Dominant Gazes Towards the Banana, Does the Subordinate Gaze Towards the Banana?

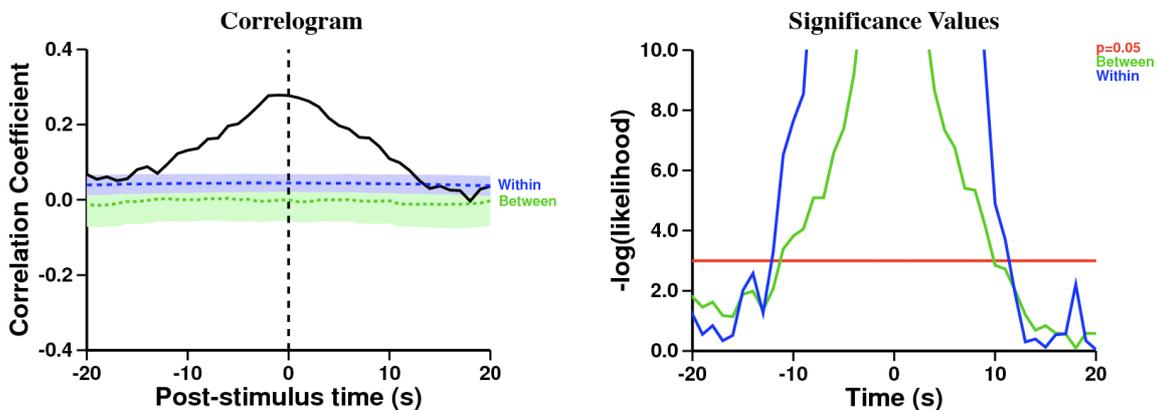


FIGURE 7.59: Referent behaviour: dominant gazes towards banana. Target behaviour: subordinate gazes towards banana. After the dominant gazed towards the banana, the correlation coefficient of the subordinate gazing towards the banana is significantly more than expected from the within-trial shuffled control (peak at time= 0, $r = 0.2772$, $n = 1857$; $-\log\text{-likelihood} = 51.3762$, $p < 0.05$).

Cross Correlation, Pair 2 *Unequal Rewards*: When the Dominant Gazes Towards the Cucumber, Does the Subordinate Gaze Towards the Cucumber?

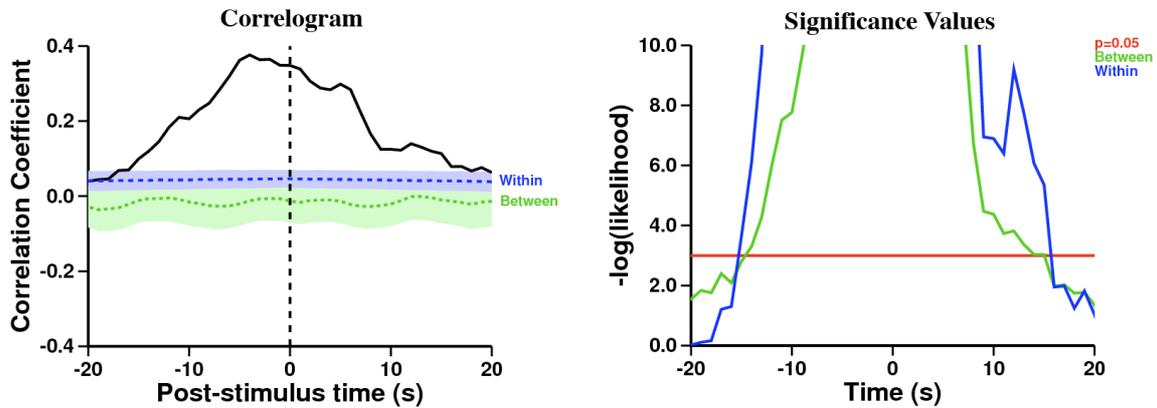


FIGURE 7.60: Referent behaviour: dominant gazes towards cucumber. Target behaviour: subordinate gazes towards the cucumber. Before the dominant gazed towards the cucumber, the correlation coefficient of the subordinate gazing towards the cucumber is significantly higher than the within-trial shuffled control (peak at time=-4, $r = 0.3762$, $n = 1781$; $-\log\text{-likelihood} = 92.4452$, $p < 0.05$).

Cross Correlation, Pair 2 *Unequal Rewards*: When the Dominant Walks Towards the Banana, Does the Dominant Look at the Subordinate and then Gaze Towards the Banana?

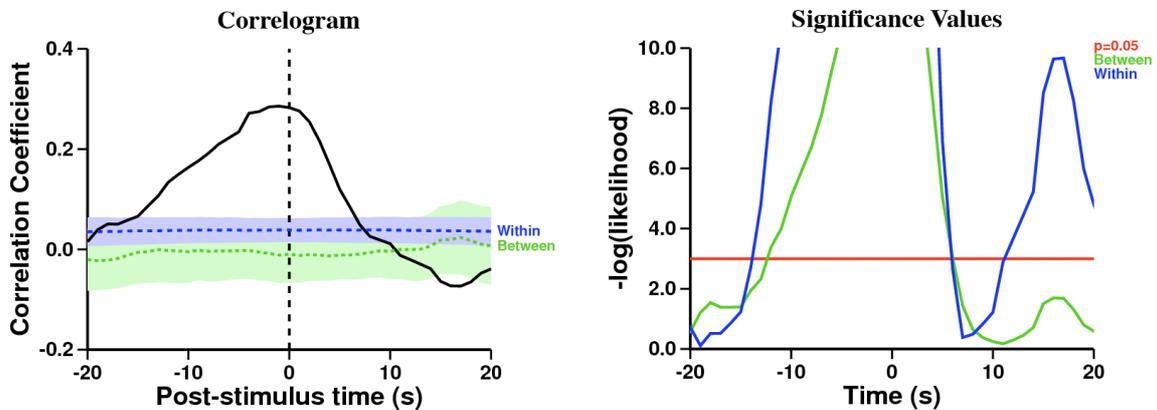


FIGURE 7.61: Referent behaviour: dominant walks towards banana. Target behaviour: dominant looks at the subordinate and then gazes towards the banana. Before the dominant walked towards the banana, she alternated gaze between the subordinate and the banana (peak at time= 0, $r = 0.2827$, $n = 1863$; $-\log\text{-likelihood} = 53.2790$, $p < 0.05$). After the dominant walked towards the banana, she was unlikely to alternate gaze (time= +17, $r = -0.0733$, $n = 1568$; $-\log\text{-likelihood} = 9.6671$, $p < 0.05$).

Cross Correlation, Pair 2 *Unequal Rewards*: When the Dominant Walks Towards the Cucumber, Does the Dominant Look at the Subordinate and then Gaze Towards the Cucumber?

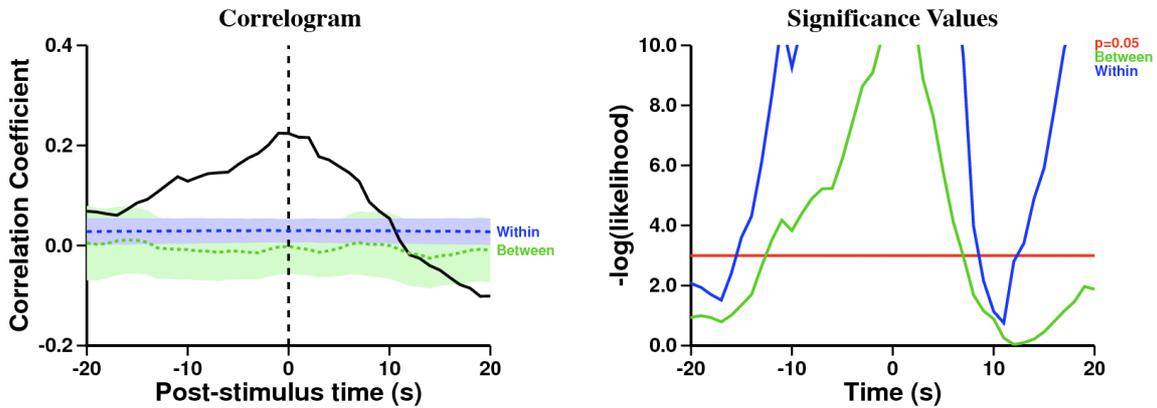


FIGURE 7.62: Referent behaviour: dominant walks towards the cucumber. Target behaviour: dominant looks at the subordinate and then gazes towards the cucumber. Before the dominant walked towards the cucumber, she alternated gaze between the subordinate and the cucumber (peak at time= 0. $R = 0.2239$, $n = 1863$; $-\log\text{-likelihood} = 35.9711$, $p < 0.05$). After the dominant walked towards the cucumber she was unlikely to alternate gaze (time= +19, $r = -0.1015$, $n = 1532$; $-\log\text{-likelihood} = 13.8027$, $p < 0.05$).

Cross Correlation, Pair 2 *Unequal Rewards*: When the Dominant Uses *Monitoring* Glances Towards the Banana, Does the Subordinate Walk Towards the Banana?

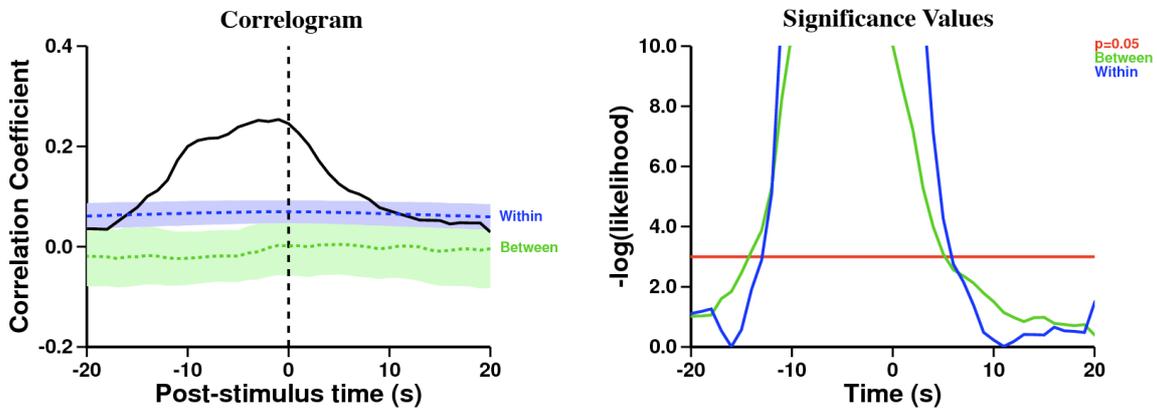


FIGURE 7.63: Referent behaviour: dominant looks at subordinate and then gazes towards the banana for two seconds. Target behaviour: subordinate walks towards banana. Before the dominant used *monitoring* glances, the subordinate was walking towards the banana (time= -1, $r = 0.2536$, $n = 1830$; $-\log\text{-likelihood} = 34.6253$, $p < 0.05$).

Cross Correlation, Pair 2 *Unequal Rewards*: When the Dominant Uses *Monitoring* Glances Towards the Cucumber, Does the Subordinate Walk Towards the Cucumber?

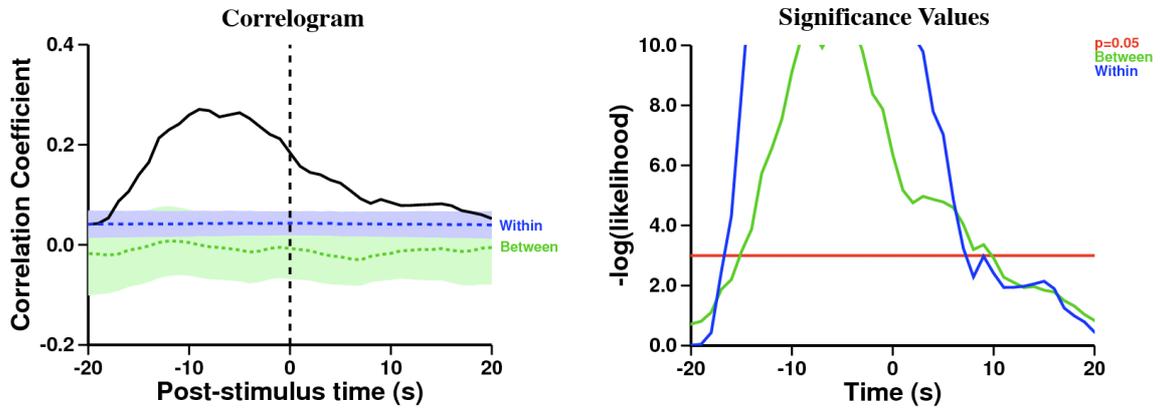


FIGURE 7.64: Referent behaviour: dominant looks at subordinate and then gazes towards cucumber for two seconds. Target behaviour: subordinate walks towards cucumber. Before the dominant used *monitoring* glances, the subordinate was walking towards the cucumber (time= -9, $r= 0.2706$, $n= 1677$; $-\log\text{-likelihood}= 42.6577$, $p<0.05$).

Cross Correlation, Pair 2 *Unequal Rewards*: When the Dominant Uses *Monitoring* Glances Towards the Banana, Does the Dominant Stop Walking?

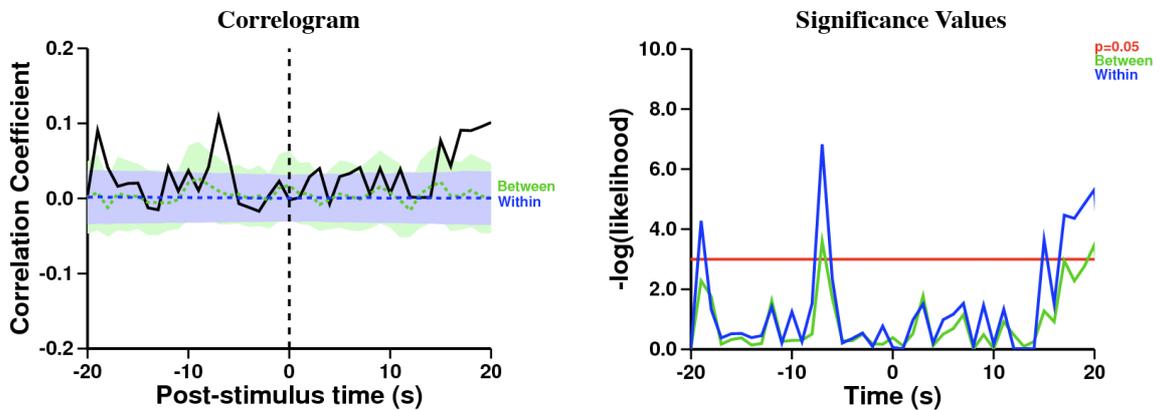


FIGURE 7.65: Referent behaviour: dominant looks at subordinate and then gazes towards banana for two seconds. Target behaviour: dominant stops walking for five seconds. Before the dominant used *monitoring* glances, she stopped walking (time= -7, $r= 0.1083$, $n= 969$; $-\log\text{-likelihood}= 6.8263$, $p<0.05$).

Cross Correlation, Pair 2 *Unequal Rewards*: When the Dominant Uses *Monitoring* Glances Towards the Cucumber, Does the Dominant Stop Walking?

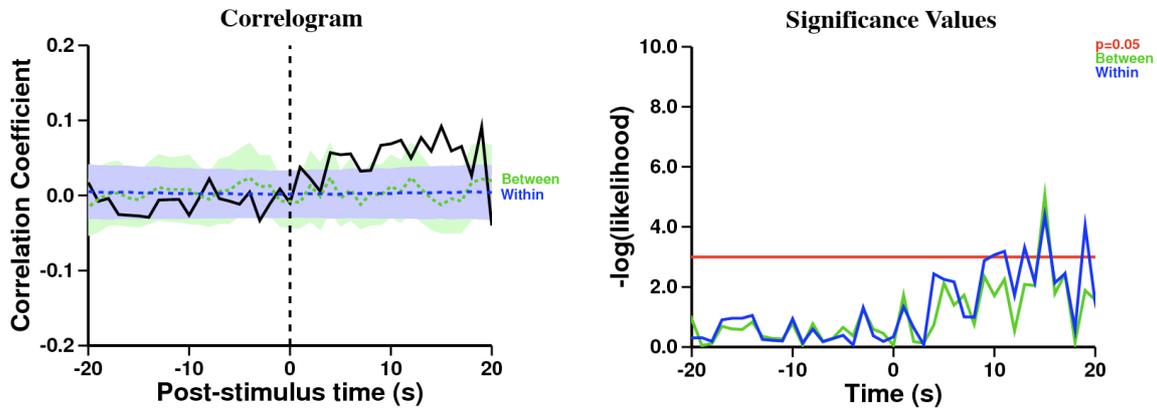


FIGURE 7.66: Referent behaviour: dominant looks at subordinate and then gazes towards the cucumber for two seconds. Target behaviour: dominant stops walking for five seconds. After the dominant used *monitoring* glances, she stopped walking (time= +15, $r= 0.0919$, $n= 766$; $-\log\text{-likelihood}= 4.3599$, $p<0.05$).

Cross Correlation, Pair 2 *Unequal Rewards*: When the Dominant Uses *Recruitment* Glances Towards the Banana, Does the Subordinate Walk Towards the Banana?

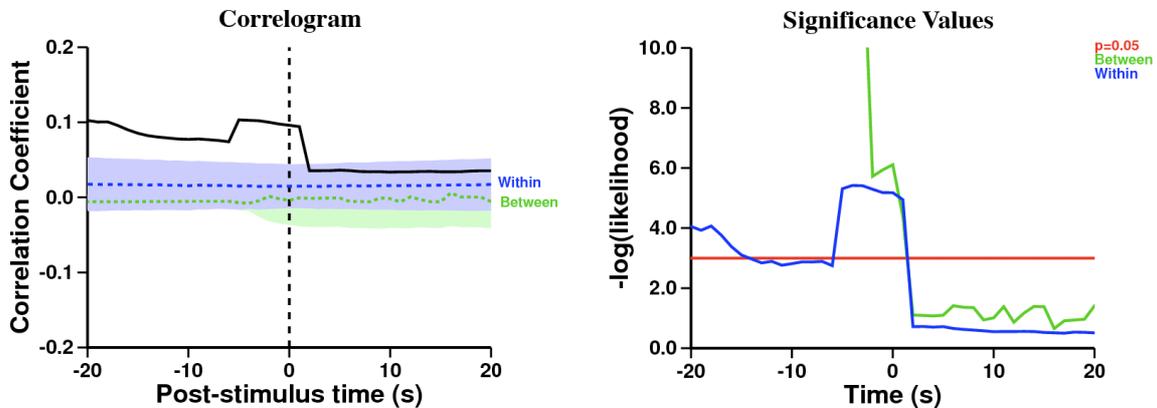


FIGURE 7.67: Referent behaviour: dominant looks at subordinate and then gazes towards the banana for two seconds and then stops walking for five seconds. Target behaviour: subordinate walks towards banana. The subordinate was walking towards the banana before the dominant used *recruitment* glances (time= -4, $r= 0.1026$, $n= 897$; $-\log\text{-likelihood}= 5.4190$, $p<0.05$).

Cross Correlation, Pair 2 *Unequal Rewards*: When the Dominant Uses *Recruitment* Glances Towards the Cucumber, Does the Subordinate Walk Towards the Cucumber?

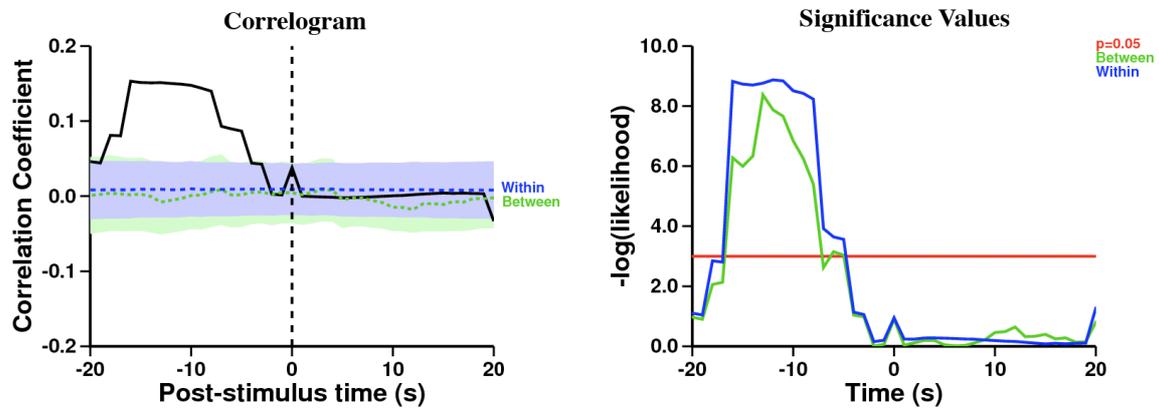


FIGURE 7.68: Referent behaviour: dominant looks at subordinate and then gazes towards cucumber for two seconds and then stops walking for five seconds. Target behaviour: subordinate walks towards cucumber. The subordinate was walking towards the cucumber before the dominant used *recruitment* glances (time= -12, $r = 0.1501$, $n = 775$; $-\log\text{-likelihood} = 8.8726$, $p < 0.05$).