#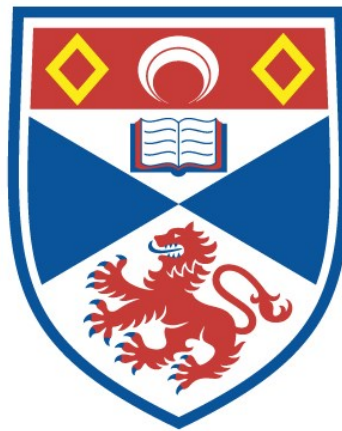 OSTENSION, PRAGMATICS, AND PRESUMPTIONS OF RELEVANCE: AN INVESTIGATION OF COMMUNICATION COGNITION IN NON-HUMAN PRIMATES

Elizabeth Warren

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Ostension, Pragmatics, and Presumptions of Relevance: An Investigation of Communication Cognition in Non-Human Primates
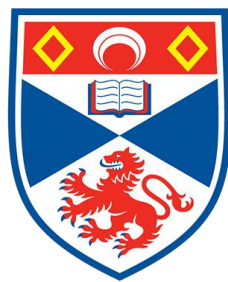
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Abstract

A prominent debate in the study of non-human primate cognition concerns their level of cognitive engagement with communication, and especially their capacity for pragmatic and ostensive communication. I investigated this question across four experiments, probing non-human primates' expectations in response to ostensive behaviour and their production of context-dependent, goal-directed gestures in a cooperative setting. In the first experiment, I examined whether chimpanzees (*Pan troglodytes*) moderated their object choice patterns based on their differentiation between ostensive and non-ostensive displays from me, a cooperative human partner. In the second experiment, I investigated whether seven species of non-human primates acquired an expectation of relevant information when they were addressed with ostensive communication, using their gaze-following behaviour as a measure. In the third experiment, I explored whether all four species of non-human great apes moderated their expectation of action from me following ostensive address, measured by their production of requesting behaviours. This experiment used varying emotional valences within the ostensive displays, in order to examine whether subjects were sensitive to the context-setting nature of emotional tone in communication. In the fourth experiment, I examined whether chimpanzees produced requesting behaviours pragmatically depending on their past experience with me as cooperative partner. The results from these four experiments showed that certain primates are sensitive to the presumption of relevance generated by ostensive behaviour, and that their responses to ostensive communication are moderated by factors such as emotional valence. These results did not suggest, however, that primates are able to compute specific informational meanings following ostensive communication, nor that they rely on mutual common ground to imbue their own communication with meaning. I interpret these findings in context with existing theories of pragmatic and ostensive communication and analyse some theoretical and empirical factors that make a paradigm suitable for the study of ostensive communication in non-human primates.

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General Introduction

1. An Overview of Pragmatic and Ostensive Communication

Animal communication is a vast and incredibly rich area of behaviour and cognition. It encompasses a multifarious suite of phenomena, from the aposematism of a caterpillar to the courtship displays of bowerbirds, to the nuanced linguistic exchanges between humans. Scientific exploration of the evolution and function of communication in animals dates back to the times of Darwin (1872/1998), who argued that the expression of emotion serves an evolved, adaptive, communicative purpose. Since Darwin and his contemporaries, the study of animal communication has given rise to numerous theories describing its ultimate and proximate functions. One particularly intriguing line of inquiry into animal communication is the question of the cognitive mechanisms and processes that support and enable it. Analysis of the complexity of an individual's cognitive engagement with communication opens a window into the evolutionary and ontogenetic development of social behaviour, from the representation of others as individual, sentient agents, to the ability to consider one's own knowledge and the knowledge state of others (Baron-Cohen, 1999). Pragmatic communication, defined here as the production and comprehension of signals which extend beyond the semantic and require context-based interpretation, is a particularly rich mine in terms of underlying cognitive mechanisms; it raises the questions about intentionality, flexibility, and inference, each of which has been debated as a hallmark of human cognitive uniqueness (Hewes, 1973; Woodruff & Premack, 1979; Gardner et al., 1989; Fischer & Price, 2017; Zuberbühler, 2018). Likewise, the phenomenon of ostensive communication, defined here as a specialized form of pragmatic communication that involves computation of communicative intentions, inspires inquiry into the complex cognitive processes that may underlie it, including integrated knowledge about the self and others (Sperber & Wilson, 1986; Wilson & Sperber, 2002; Csibra & Gergely, 2009; Gómez, 2011; Moore, 2016, 2018). Examining communication cognition in non-human primates invites consideration of the evolutionary building blocks of the capacity for pragmatics and ostension. It allows insight into the ecological and social pressures that may have favoured the evolutionary development of cognitive mechanisms required for pragmatic communication and helps illuminate the social strategies of non-human primate species when solving everyday puzzles such as collective travel, cooperative hunting, and navigation of individual social relationships.

Pragmatic communication is a valuable lens through which to examine flexible and nuanced communication in both humans and non-human primates. It provides a benchmark of complexity by which to evaluate the level of cognitive engagement in any given communicative exchange. Ostensive communication – the expression and comprehension of communicative intention, which triggers key assumptions that an exchange is informative and relevant – is an even higher bar within the realm of pragmatics (Csibra & Gergely, 2009; Wilson & Sperber, 2002), one that some authors suggest is unique to humans (e.g., Scott-Phillips, 2016; Fischer & Price, 2017; Townsend et al., 2017). A predominant challenge in the comparative study of pragmatic and ostensive communication is that the definition of each, and especially of ostension, is varied and divergent across different fields examining the same phenomenon. Although the fields of philosophy of language, developmental psychology, and comparative psychology have amassed extensive theoretical and empirical work on ostension (detailed below), there is no universally accepted understanding of exactly what it means, or exactly what it looks like, to be ostensive in communication. This is a particular concern when distilling the theoretical perspectives on ostension into practical methods than can assess it in non-linguistic (or pre-linguistic) subjects. Characterizing the

nature and purpose of ostension, especially for application in non-human species, is an unsolved problem in comparative cognition. Dominant theoretical work does not specify clear, undisputed behavioural markers of production or comprehension of ostension, other than linguistic reporting of nuanced meaning (Montgomery, 2005; Scott-Phillips, 2014). In this thesis, I will explore, design, and apply empirical paradigms for the study of pragmatic and ostensive communication in non-human primates. I will link my measures of ostension and my interpretation of my findings to the theoretical philosophies of pragmatic communication, but also to methodological considerations for assessing communication cognition in a practical setting.

1.1 Pragmatic Communication

In the context of this thesis, I define pragmatic communication as communicative behaviour which is context-dependent – it relies on situational factors to imbue and interpret its meaning. In humans, pragmatic communication can be expressed as everything that is *meant* by the communicator, as opposed to just everything which is *said* (Bavelas, 1992; Kelly, 2001; Scott-Phillips, 2014). The producer and the recipient may both use accompanying signals such as vocal inflection, body language, and facial expression to give context to utterances with multiple possible interpretations, and may likewise take details such as past experience with each other and cues from the surrounding environment to create or gain a full understanding of the communicator's meaning (Clark & Carlson, 1981). In non-human primates, pragmatic communication may include the differential use or interpretation of the same communicative behaviour depending on context such as activity (e.g., feeding, travelling, fighting, play), motivation (e.g., competition, cooperation), or relationship (e.g., parent-infant, courtship, tolerant non-kin). Importantly, I differentiate this definition from voluntary and intentional communication (see Byrne et al., 2017, see below for further discussion of intentional communication), which may be flexibly produced, but is not pragmatic, in the following manner: communication may be produced, combined, or supressed partially under the voluntary control of the individual, but still adhere to fixed, semantic meanings with no moderation to the meaning drawn from the context, and thus, no pragmatic interpretation is required (e.g., Arnold & Zuberbühler, 2006; Crockford et al., 2015). Similarly, communication may be used in an intentional and goal-directed manner, but not subject to situational inferences made during production and comprehension, rather based on learned associations of whether the signal will or will not be successful (e.g., if the recipient is visually attending to the signal, if the recipient is showing aggressive or tolerant behaviour, if the signal has been successful in similar past interactions) (e.g., Leavens et al., 2010; Cheney & Seyfarth, 2018). For a more detailed breakdown of the differences between flexible, intentional communication and inferential, pragmatic communication, see Chapter 3.

1.2 Fixed versus Flexible Communication in Non-Human Primates

In early accounts detailing the communicative behaviours of wild primates (e.g., Goodall, 1986; Kummer, 1968), researchers were not certain as to the extent to which communicative signals of great apes were produced intentionally. Prevailing literature on primate vocalizations suggests that the majority of vocal signals in great apes tend to be fixed – always relating to the same behavioural actions or responses – and often reflexive, meaning they are induced by arousal and are not under the voluntary control of the individual (Arbib et al., 2008; Fröhlich, Sievers, et al., 2019; Seyfarth et al., 1980; Seyfarth & Cheney, 2003).

There is not strong evidence to suggest that most vocal signals within species' repertoires are socially learned, nor do the vocalizations develop in form over time, although it has been observed that certain signals, such as referential food grunts in chimpanzees (*Pan troglodytes)*, may be modified by vocal learning (Watson et al., 2015). There is some evidence that certain vocal signals are under the voluntary control of individuals, such as observations of wild baboons moderating whether or not they produced reconciliatory grunts following a threat from a conspecific (Cheney & Seyfarth, 1997). Furthermore, it has been observed that baboons can modify some aspects of vocal signals, such as duration, depending on the situation, and that these modifications affect interpretation on the part of the recipient (Seyfarth & Cheney, 2010). Although these findings suggest that primate vocalizations can sometimes be intentional, it remains that the majority of primate vocal signals are relatively innate, which limits their potential to act as building blocks for complex, intentional communication (see Wheeler & Fischer, 2012, for review).

Research into the gestural domain, on the other hand, has shown that gestural communication in primates is rich with intentional, flexible signals that may bespeak cognitive mechanisms for complex, pragmatic communication, especially in great apes (Plooij, 1978; Tomasello et al., 1985, 1994; Hobaiter & Byrne, 2014; Tomasello & Call, 2019). Early studies, such as Woodruff and Premack, (1979) found evidence that apes could flexibly produce or withhold behavioural cues to inform a researcher of the location of a hidden reward, depending on whether they believed that the researcher would cooperate or compete with them, respectively. This finding suggested that great apes could, at the very least, make intentional decisions about when and how to communicate with gestural signals. Observational analyses of the gestural repertoires of all four species of great ape and certain species of small apes show that each uses a rich repertoire of gestures flexibly and in goal-directed ways, with variation in gesture type and frequency according to circumstantial conditions (Pika et al., 2003; Liebal, Pika, & Tomasello, 2004; Pika, Liebal, & Tomasello, 2005; Liebal et al., 2006; Pika & Mitani, 2006). Modern work has demonstrated that the same hallmarks of intentional, goal-directed communication identified in humans – gaze-alternation, monitoring of attention, persistence, and elaboration (Bretherton & Bates, 1979) – are present in non-human primate communication (see reviews by Leavens et al., 2005; Liebal et al., 2014; Graham et al., 2020). Many authors have suggested that the evolutionary origins of the open-ended and flexible nature of human language are found not in vocal communication, but in gestures (e.g., Corballis, 2008; Liebal & Call, 2012; Fröhlich, Sievers, et al., 2019).

1.3 Pragmatic Communication in Non-Human Primates

While intentionality and goal-directedness alone are not enough to suggest pragmatic, inferential communication, some evidence suggests that primates are able to make situational inferences about their partner's knowledge state when they produce imperative (requesting) gestures or about their partner's goals when they interpret the actions of a human experimenter. In terms of awareness of a partner's knowledge state, great apes have been shown to produce requesting gestures selectively based on previous interactions, wherein apes flexibly requested absent food rewards according to their past experience with a specific human (Bohn et al., 2015, 2016b). In this study, subjects pointed to the location of absent (already consumed) food, preferentially over a still available lower-value food, only in conditions when the present researcher knew the previous contents of the now empty plate and had shown willingness to retrieve it in the past. In addition to differential pointing based on their partner's knowledge state, apes in this experiment demonstrated the subjects'

apparent expectation that the human would be able to interpret this cue from context, as it is not normally rational to point to a location without food. Zimmermann et al. (2009) showed that great apes are able to flexibly use pointing gestures to inform a human about the location of a hidden tool used to retrieve food. Subjects pointed to the location of the tool, as opposed to the location of the desired food, significantly more in conditions where the tool was necessary to retrieve the food. They also differentiated their pointing behaviour based on whether the human was knowledgeable as to the location of the tool, pointing more often when the cooperating researcher had not been the one to hide the tool. These examples of intentional, referential, context-moderated gestures in great apes lend credence to the idea that they are capable of producing communicative behaviour that would be irrational if they did not expect the human experimenter to make inferences about what they meant. Regarding non-human primates' sensitivity to context in terms of comprehension, great apes have been shown to adjust their willingness to wait for a human's actions based on their interpretation of the human's goal, the human's ability to act, or the human's motivation (Buttelmann et al., 2012; Call et al., 2004; Call & Tomasello, 1998, respectively).

Great apes' ability to produce pragmatic, context-based communicative signals has also been documented in the form of "attention-getting" gestures, used to recruit the attention of their audience (Tomasello & Call, 2019, for review). It has been suggested that attention-getters, which comprise both visual signals with an auditory component, such as ground-slapping, and tactile signals, such as placing an arm around the recipient, function to recruit visual contact with the recipient, before making a visual, referential gesture (Liebal, Call, Tomasello, et al., 2004). At a glance, this explanation of attention-getting gestures supports the idea that apes use their gestures intentionally but does not necessarily suggest that they use gestures pragmatically, where the recipient must rely on context to interpret the meaning, since a referential gesture follows the attention-getter. In certain instances, however, great apes have been recorded using these same "attention-getting" signals when the target audience is already visually oriented toward them (Liebal, Call, & Tomasello, 2004). Given that great apes have been shown to be sensitive to whether their communicative recipient is visually attending to them (Hostetter et al., 2007), recruitment of visual contact does not appear to be the primary motivation of the "attention-getting" gesture in this context. It is possible, therefore, that "attention-getters" may also serve a more flexible communicative purpose, and could perhaps be used to add emphasis, insistence, or elaboration to referential signals, which would place them in the area of pragmatic communication. Pragmatic communication is characterized by situational inferences - the producer and the recipient use variations in the manner of communicative signalling – tone, shape and style of gestural signals, body language – and also the context of the interaction, such as competition or cooperation, to infer the rational meanings of each other's behaviour. For more detail on the relationship between inferences not based on associative learning and pragmatic communication, see Chapter 3.

1.4 Ostensive Communication

1.4.1 Relevance Theory

Ostensive communication demands comprehension of a very specific form of context – communicative intention (Sperber & Wilson, 1986; Wilson & Sperber, 2002; Moore, 2016 Heintz & Scott-Phillips, 2022). In ostensive communication, the producer intends not only that the recipient acquire certain information, but also that the recipient knows they are

communicating it to them. The manifestness of the communication – the mutual awareness that the producer intends for the recipient to know the information – recruits the recipient's power of inference to rationalize otherwise opaque or meaningless behaviour. For example, human behaviours such as suggestive looks or sarcastic eye rolls are only fully interpretable if both parties are aware that the behaviour is communicative, and thus use their mutual past experience, factors in the situation at hand, and knowledge of each other's mental state to make rational inferences about the referent and meaning behind the gesture. Theoretical philosophy of ostensive communication dates back to Grice (1957, 1969, 1989), who outlined a theory to define meaning and intention in pragmatic communicative exchanges. Grice defined communicative acts as those which do not have natural meaning; it is only because they are overtly communicated that they can be meaningfully interpreted. Following from his foundational work, Sperber and Wilson developed relevance theory (Sperber & Wilson, 1986; Wilson & Sperber, 2002), a model of ostensive communication that realizes Grice's maxims in a cognitive context, and outlines processes and hypotheses that follow from his framework. Relevance theory focuses on the inferential nature of ostension and the cognitive capacities for intention, mental state attribution, and tendency toward relevant interpretation that make it possible. Meaningful communication, as defined by relevance theory, requires twofold intentionality. The communicator must have an informative intention – essentially the information to be exchanged or the response desired from the recipient. That informative intention must be combined with communicative intention – defined as the intention that the recipient know that the communicator intends them to know the informative intention. The communicative intention influences the meaning of the message itself by triggering in the recipient a "presumption of relevance" that whatever information follows or is contained in the behaviour will have a rational meaning that is relevant to the current interaction or situation. The ability to rationalize otherwise ambiguous or nonsensical communicative signals through pragmatic interpretation lifts human communication systems out of what might otherwise be a fixed, literal, semantic code (Horn & Ward, 2008). In humans, nearly any behaviour can be made ostensive, if it is performed in a manner that makes it clear that it is addressed to the recipient. The matter of "addressing" is crucial – the fact that the communicator intends the recipient to know that they are addressing them adds additional meaning to the message (Wilson & Sperber, 2002). Comprehension of ostensive behaviour demands that the recipient be able to perceive this communicative intention and presume that they are being addressed for relevant purposes, allowing them to use contextual cues to interpret the full meaning.

1.4.2. Natural Pedagogy

Relevance theory discusses ostensive communication primarily in the context of episodic, individual interactions. The purpose of addressing a communicative partner ostensively is to induce their inferential interpretation of the communication. In an effort to identify the developmental drivers of ostension, Csibra and Gergely (2009), established the theory of natural pedagogy, a view that interprets the processes established by relevance theory through the lens of purpose: ostensive communication is an adaptation for the transmission of generalizable social or cultural information. They observed that the presumption of relevance associated with communicative intention shifts the social learning biases of the recipient and induces them to generalize the depicted behaviour to future situations (Csibra & Gergely, 2007; Gergely et al., 2007; Futó et al., 2010). Essentially, natural pedagogy examines ostensive communication through its social learning function – the effect of addressing a behaviour to the recipient changes their interpretation of the act from an observational understanding of another's goal to a cultural understanding of correct or in-group behaviour.

A proficient recipient of ostensive communication will interpret otherwise irrational behaviour (e.g., cultural dining practices that are less efficient than eating with the fingers) as relevant and purposeful, and reproduce the behaviour themselves, because they have been primed by the producer's communicative intention. In this sense, natural pedagogy poses a possible explanation for the ontogenetic development of sensitivity to communicative intention – it is a mechanism by which to acquire knowledge relevant to survival and to learn important in-group behaviours.

1.4.3 Cognitive Prerequisites of Ostension

In both relevance theory and natural pedagogy, ostensive communication is hypothesized to rely on a few cognitive prerequisites which enable the rational production and interpretation of communicative behaviour. The first prerequisite, which is critical for establishing relevant context, is common ground, is defined here as knowledge or experiences shared between two or more individuals, which can then inform the meaning of their communication (Clark, 1996; Tomasello, 2008a). Crucially, for common ground to be mutual between two parties, both must know that the information is shared knowledge, and both must be aware that the other party knows the information is shared as well. When this mutuality is in place, the producer can use mutual common ground as context to inform the meaning of an otherwise ambiguous gesture. In a traditionally Gricean understanding of pragmatics, communication is an inherently cooperative act, which induces the communicating parties to presume that the other is conveying a relevant message, and leveraging common ground to do so (Grice, 1969; Sperber & Wilson, 1986). Mutual awareness of common ground and overt manifestation of communicative intention are both hypothesized to function via theory of mind, or the ability to represent the mental state of another (Premack & Woodruff, 1978). Also called mental state attribution, theory of mind describes the capacity to think about the knowledge state, desires, motivations, beliefs, and perspectives of others (for review, see Krupenye & Call, 2019). According to both relevance theory and natural pedagogy, successful production and receipt of communicative intention require recursive theory of mind – individuals must represent their own mental state, the mental state of the other, and the knowledge that each knows the mental state of the other (Scott-Phillips, 2015; Heintz & Scott-Phillips, 2022; but see Moore, 2017 for a dissenting view of the necessity of theory of mind in ostension). Only through mental state attribution can each party manifest the overtness of the communicative intention and parse the relevant elements of the common ground between them, to discern meaning.

Although both dominant theories of ostensive communication share an understanding of what communicative intention is, and some of the cognitive prerequisites that it requires, they diverge on what it is *for*. Relevance theory views ostension as a device of communication, which enables the flexibility and nuance observed in human linguistic communication (Wilson & Sperber, 2002). Natural pedagogy characterizes it as a capacity developed for the purpose of behavioural transmission (Csibra & Gergely, 2009). In empirical work on ostension, where the theoretical processes must be made measurable and observable, this is a relevant difference. Where relevance theory generally looks toward accurate comprehension of meaning as a measure of comprehension of ostension, natural pedagogy looks to changes in the subsequent behaviour of the recipient, such as decisional biases or acquisition of skills. From the production side, relevance theory looks for evidence of the manipulation of the overtness of communicative intention – behaviours that enhance or disguise the communicative nature of the act (e.g., Grosse et al., 2013). Natural pedagogy looks for "markedness" – distinct differences of exaggeration, inefficiency, or tone that set

communicative intention apart from non-communicative actions (Gergely & Király, 2019). Although most empirical studies of ostensive communication are guided by one of the two major theoretical orientations above, there is not a unifying, systematically applicable method to identify communicative interactions as ostensive or otherwise.

1.5 Ostensive Communication in Non-Human Animals

The theoretical work on pragmatic and ostensive communication originated in the area of human cognition, focusing on acquisition and comprehension of language, and thus semantic, linguistic signals were included as part of the equation for meaningful communication. Much of the behaviour used in pragmatic communication, however, is flexible and intrinsically ambiguous – not composed of codified signals (see Tomasello, 2008a, for overview). In some interactions, the role of context is so profound that semantic signals are not necessary for the communication to be successfully interpreted. As theoretical work on communication cognition has developed, some researchers argue that since linguistic signals are not a mandatory aspect of pragmatic communication, it is possible that context-based communicative behaviour can be observed in non-linguistic subjects, such as non-human primates. The challenge of defining and measuring ostension is even more pronounced in the field of comparative cognition than it is in the fields of developmental psychology and philosophy of language. Although both relevance theory and natural pedagogy have been adapted to non-human species, both are based on linguistic communication, and are therefore oriented toward human communicative and social behaviour. Practical measures of ostension derived from these theories are often based on human-specific behaviours, such as pointing, or are reliant on the comprehension of specific linguistic meaning. There is discord between authors in comparative psychology as to what constitutes analogous ostensive behaviour in non-humans, and empirical findings are consequently difficult to compare between species, and particularly difficult to compare to humans. A top-down approach to comparative ostension, where tasks to assess ostension in humans are adapted to animals, tends to produce particularly limited comparisons, given that the tasks may be based on expectations formed from human behaviour. Equally, some authors have criticized non-human-centric approaches to ostension as shallow or diluted versions of the complex cognition involved in ostensive communication, and point out that comparisons between non-equivalent theoretical frameworks are likewise limited (e.g., Scott-Phillips, 2016).

Research into ostensive communication in non-human animals, especially primates, has spanned anecdotal instances of apparent communicative intention, empirical investigations of animals' comprehension of meaning, and theoretical analyses of the merit of a line of inquiry into comparative ostension. Gómez (1996) was the first to publish work on ostension in non-human animals, applying a Gricean interpretation to his observational accounts of eye contact during communicative behaviour between enculturated gorillas (*Gorilla gorilla)* and their human caretakers. These observations built on contemporary observational work on the non-threatening functions of eye contact in primates (Goodall, 1986; de Waal, 1989), where eye contact appeared to help facilitate reconciliatory acts. Gómez (1996), however, noted the role that eye gaze played in imperative demands apes produced for humans, and posited that deliberate eye contact in certain cooperative exchanges serves not just to acquire the attention of the recipient, but to direct it toward the contents of the signaller's attention. He suggested that this manipulation of joint attention toward subsequent imperative gestures extends beyond codified communicative exchanges and into referential addressing of a communicative partner. Intentional eye contact, in this context, expresses the signaller's

communicative intention to transmit an imperative request. Of particular theoretical significance, Gómez suggests that this is means of circumventing the potential lack of shared gestural repertoire between apes and humans – the apes were able to bypass the inability to use codified, semantic gestures that might have been poorly understood given the lack of shared repertoire between apes and humans, and use a more flexible, pragmatic system of directing attention and relying on inference.

In a review of work continuing to define and probe ostensive behaviour in non-human animals, Pika (2012) presented further accounts of referential, ostensively produced animal behaviours that resemble early evidence of ostension in humans. Citing evidence from not only non-human apes, but also corvids, the review pointed to actions such as "showing," (Pika & Mitani, 2006) "offering" (Pika & Bugnyar, 2011) and "pointing," (Veà & Sabater-Pi, 1998) as systematic evidence of referential gestures in multiple species, and noted that those same gestures are accepted as early indications of ostensive-inferential communication in infant humans. Pika's work highlights the importance of the gestural domain to explore non-codified, referential signals, and opens the door for investigation of ostension in multiple species, using these broader, non-linguistic means of referential signalling. This review also illustrates the challenge of forging direct comparisons between linguistic humans and non-linguistic animals, while maintaining the integrity of the theoretical complexity of ostension. The theoretical validity of behavioural measures of ostension in animals will inherently be called into question if the behaviour does not appear to be drawn from the same prerequisites that are presumed in human ostensive communication – namely, recursive theory of mind.

Another approach to the theoretical question of ostension in animals, taken by Moore (2016, 2017), has been to challenge the presumed cognitive prerequisites to ostensive communication – namely the necessity of recursive, fourth-order theory of mind. Moore argued that the use of eye contact in ape and human communication is outwardly similar, but interpreted differently between the two species, given the presumed cognitive complexity of ostension and the relative lack of evidence of metacognitive abilities such as mental state computation in apes (for review, see Kaminski et al., 2008). In a continuation of Gómez's (1996) suggestion that apes' command of attention satisfies Grice's second clause – the requirement of communicative intention – Moore proposed that the use of "attention-getter" gestures (for review, see Tomasello et al., 1997), including intentionally established eye contact, is evidence of the intentional address necessary for ostensive communication. This argument demonstrates an important dilemma regarding the integrity of comparisons between human infants and non-human primates: we cannot conduct meaningful analysis of the relative cognitive abilities between species without measurable behaviours that can be accepted as evidence of that ability in both species. Moore (2017) addresses this point, noting that models of ostensive communication in humans may be "intellectualizing" ostension to include the assumption of high-order theory of mind, but without specific behavioural evidence of this prerequisite. When this assumption is dropped, the grounds to reject a Gricean structure to great ape communication become much weaker.

Moore (2016) also refutes the idea that great apes' generally poor comprehension of human communicative intention produced in the form of pointing (see reviews by Tomasello, 2008b; Halina et al., 2018), can be taken as evidence that apes are unlikely to comprehend communicative intention altogether. Drawing on reviews of pointing in apes such as Leavens (2005), Moore summarizes the argument that pointing is not a suitable comparative measure of ostension, given that it is rare or absent in the natural gestural repertoire of apes, and follows a different ontogenetic development to human pointing even when it does appear in

captive ape populations. The issue of pointing as a line of inquiry into ostension in animals fits into the broader matter of comparable behavioural measures between species; ideally, measurable behavioural evidence of ostension must be a) presumed to represent the same level of cognition in any species to which it is applied, and b) congruous with the behavioural repertoire of the species in question, rather than automatically derived from human behaviour.

While the majority of the work on ostension in non-human primates is founded in relevance theory or directly in Grice's maxims, a substantial portion of the work on ostension in canines follows from natural pedagogy. Topál et al. (2014) distinguish between the two theories, noting that relevance theory is founded in linguistics, while natural pedagogy is founded in social learning. As such, the genericity bias associated with natural pedagogy may be more easily compared between species as a measurable outcome of ostension, given that it does not rely on a system of language or a specific set of behaviours or gestures. For example, Topál et al. (2009) confirmed that domestic dogs show sensitivity to human ostensive cues such as eye contact and "motherese" in a social learning context; they were more likely to persevere with a choice that had been ostensively displayed to them, even if they knew it to be incorrect. Topál et al. (2014) found that there is not empirical evidence that canines generalize ostensive displays outside of the immediate social learned context, which is evidence against the more cognitively complex comprehension of ostensive communication seen in infant humans. Unlike the failure of apes to comprehend ostensive pointing displays, however, this lack of evidence is not as easily dismissed by differences in the vocal or gestural repertoire, since dogs were shown to be sensitive to the same ostensive cues in more immediate contexts.

Although the study of comparative ostension has expanded over the past 25 years, some authors reject the application of Gricean structure to animal systems of communication. These objections fall into two main camps: either theoretical disagreement with the evidence for ostension in animals, or criticism of the default to direct comparisons between humans and animals. Both of these stances hinge on the question of mental state attribution in communication. Scott-Phillips (2015), argues that recursive theory of mind is a necessary mechanism of communicative intention. He makes a case for differential interpretation of behaviours like eye contact between preverbal infants, who will, in normal ontogenetic development, be capable of fourth-order theory of mind, and apes, for whom there is scarce evidence of the same capacity. In more recent work, Heintz and Scott-Phillips (2022), argue that evidence of intentional and pragmatic social exchanges in non-human primates does not rise to the level of ostensive communication for a similar reason – a lack of evidence for the "complementary" mechanisms of communicative intention from the producer and presumption of relevance triggering inferential interpretation in the recipient. On the other hand, authors such as Bar-On (2013) and Townsend et al. (2017) have criticized the top-down approach to investigations of communication, focussing instead on the evolutionary building blocks of communication systems and redirecting theoretical work toward the intentional communication observed in non-human primates. Their view holds that measuring animal cognition using theoretical frameworks based on linguistic humans may be an inefficient line of inquiry to discern origins and underpinnings of complex communication in animals. This argument rejects the focus on mental state attribution and rational inference, noting that direct comparisons with humans will always find non-linguistic species lacking, and instead promotes a bottom-up framework for investigating communicative behaviour.

Current approaches to comparative ostension have yielded some empirical evidence in great apes, corvids, and canines, albeit using definitions of ostensive behaviour not universally agreed upon by all theoretical frameworks. In addition to the above work by Gómez (1996 see also Gómez, 1994, for similar investigations in chimpanzees), investigations have found evidence that ostensive signals enhance attention in chimpanzees, compared with attention-getting, non-communicative displays, indicating some sensitivity to ostensively produced cues (Kano et al., 2018). They do not, however, enhance meaningful interpretation of an actor's gaze, suggesting that full interpretation of communicative intention, following the theoretical framework laid out by relevance theory, is not in effect. As with theoretical limitations to interpretation of apes' failure to comprehend pointing, the authors note that inter-specific communication may limit the possibility that non-enculturated apes will interpret relevant meaning from a human actor. From a social-learning angle, Marno et al. (2022), found that chimpanzees were more likely to use a tool that had been ostensively demonstrated to them, regardless of whether it successfully operated a device, then a non-ostensively demonstrated tool, even when the non-ostensively demonstrated tool was known to the apes to be functional. This suggests that, like domestic dogs (Topál et al., 2009), chimpanzees may be sensitive to human ostensive cues as they relate to the transmission of information.

In canines, in addition to the previously mentioned work by Topál et al., Tauzin et al. (2015a,b) found that domestic dogs were sensitive to the order of ostensive sequences, and were able to derive "where" information when a directional point followed an ostensive cue, but not when the point preceded the ostensive signal. This suggests that ostensive address by humans may raise canines' expectations of relevant information to follow, in line with natural pedagogy as an explanation for the function of ostension. Some of the empirical work with canines has produced evidence against more complex engagement with ostension; Moore et al. (2015) found that although dogs were sensitive to ostensive cues produced with the human actor's body (e.g., pointing), they failed to comprehend ostensive cues produced using an apparatus. The authors suggest this indicates that domestication may have supported some sensitivity to human-produced ostensive cues, while not facilitating an inherent presumption of relevance across any type of communicative display. Similarly, Neilands et al. (2021), found that dogs were not able to correct an A-not-B error following social scaffolding such as pointing or demonstration, and suggest that although dogs may be sensitive to some ostensive cues, their finding supports the notion that ostensively facilitated social learning is a uniquely human adaptation.

2. Empirical Considerations in the Study of Ostension

It is worth noting that many of the above empirical investigations into ostensive communication in animals share a few key traits: they are conducted using interspecific exchanges between humans and animals; they are based on hypotheses founded in either relevance theory, natural pedagogy, or a combination of the two; and they concern a top-down approach where the animal species is compared (often directly, within the same study) to preverbal human children, and measured against expectations formed from human behaviour in the same or a similar scenario. Some of these factors are difficult to change – for instance, it is nearly impossible to conduct a controlled experiment with specific ostensive displays between conspecific individuals, unless one of the animals is a highly-trainable individual who still has good social relationships with conspecifics. When the ostensively communicating partner is a human, however, the presumption of common ground is all the

more elusive, when there is not even a fully shared repertoire of communicative behaviours from which to draw. Conversely, observational accounts, while not encumbered with the challenges of inter-specific communication, are difficult to control, and therefore difficult to differentiate from other possible explanations of the flexible communicative behaviour. Additionally, observational work is beholden to a different interspecific problem – identification of any ostensive behaviour falls to the human observer, who may miss behaviours that are outside the human-derived expectations of ostension. It is challenging to let go of human-oriented perspectives on ostension and construct a bottom-up paradigm that examines changes in naturally occurring behaviours and biases on the basis of ostension. It is especially difficult to create such an experiment while still adhering to the richer and deeper requirements of theory of ostension; that is, without taking a shallower, narrower definition of ostension so as to investigate it in non-human species. This challenge forms the basis for the program of research in this thesis – I attempt to probe the capacities for pragmatic and ostensive communication in non-human primates, using methodology that is less confounded by expectations from the human experience of ostension, but which does not sacrifice the richness and cognitive complexity of mentalized, inferential communication.

3. Objectives of the Current Study

The objectives of this research were as follows: first, I aimed to investigate sensitivity to ostension in non-human primates (hereafter "primates") by examining whether their expectations about subsequent events change as a result of their comprehension of communicative intention. Within this question, I aimed to tease out some of the factors that may or may not contribute to the effects of ostension: the effect of enhanced attention from addressing, the effects of varying emotional valences of ostensive displays, and the effect of my availability, as the communicating human partner, to receive communication following my ostensive display. Second, I aimed to investigate whether primates produce communication behaviours pragmatically based on their past experience with a partner, which is a key component of the ability to wield common ground in communicative exchanges (Nunberg, 1978; Scott-Phillips, 2017). Third, I aimed to design bottom-up paradigms to investigate the production and comprehension of pragmatic and ostensive communication in non-human primates. I sought to use tasks and behavioural measures that manipulated primates' natural, unsolicited, untrained reactions to stimuli, and I looked to behaviours and biases from the natural ontogeny of primates to set the parameters of the tasks, rather than modifying tasks originally designed to assess ostension in human infants.

In this thesis, I present five investigations of pragmatic and ostensive communication in non-human primates. First, I designed and ran a task which assessed whether chimpanzees can correctly infer the location of a hidden food reward based on ostensive communication, and whether they did so differentially compared to a non-ostensive display. This task was reminiscent of the top-down methods described above and provided a benchmark by which to evaluate the validity of certain task demands, such as the comprehension of declarative intention. Second, I conducted a theoretical analysis of the concept of inferential communication, and the cognitive processes therein. I sought to provide a narration of the possible cognitive mechanisms at play during pragmatic, flexible communication that surpasses the bounds of intentional communication but does not rise to the level of ostension. I highlight the different complexities of social inferences that may be made during communicative exchanges and put forward a new proximate model of communication – inferential communication – as a framework through which to investigate pragmatics and flexibility in animal communication.

Third, following this theoretical analysis of inference and pragmatics, I investigated whether non-human primates are sensitive to the relevant and information-carrying nature of ostensive communication, using changes to their gaze-following behaviour as a measure of their expectation of information. I looked to differentiate between the effects of enhanced attention and the effects of ostension on primates' expectations in order to determine whether ostension acts on their mental states through the route of communicative intention, rather than stimulus enhancement. Fourth, I expanded my investigation of the effects of ostension on primates' expectations by examining whether variation in the emotional valence of ostensive displays differentially moderated the effect of ostensive address. Here, I used impatience and requesting behaviours as a proxy for expectation of action from me, a cooperating partner, and measured whether those expectations were raised or lowered by ostensive displays with opposite emotional contexts. Finally, I examined the production of pragmatic communication in chimpanzees, looking at whether past experience with a cooperative human partner moderated their rate of impatience and requesting behaviours. Following my summary and analysis of the findings from these investigations, I discuss some overarching takeaways and suggest some methodological considerations for the study of pragmatics and ostension in non-human primates.

Chapter 2 Proto-Presumptions of Relevance in Chimpanzees

Abstract

A focal question in the study of pragmatic communication in non-human primates is whether they are capable of understanding and drawing relevant inferences from ostensive communication. Probing primates' performance in adapted versions of communication tasks for human children can provide a valuable benchmark to begin to assess the capacity for ostension in a non-linguistic species. This study investigated whether chimpanzees distinguish between ostensive and non-ostensive behaviour from a human experimenter, where both displays contain referential cues and social stimulus enhancement, but only the ostensive display includes communicative intention and is addressed to the subject. I presented eight chimpanzees with a choice between two possible food locations, in which each location was displayed, either ostensively or non-ostensively, within the same trial. The prediction in this experiment was that, if subjects are capable of comprehending communicative intention, they should make rational inferences about the location of the food reward from the experimenter's behaviour, and their search strategy should be biased toward the ostensively-displayed location. The results of this experiment showed no bias toward ostension; subjects chose at chance between the ostensively and non-ostensively displayed food locations and adopted a distinctly side-biased search strategy in both the experimental and control (no displays at all) conditions. These results suggest that the subjects did not differentially presume relevant information-sharing from the experimenter's ostensive display, and therefore do not support the hypothesis that chimpanzees are able to comprehend communicative intention. Given the practical limitations and theoretical weaknesses of this and similar paradigms, however, this task may not have been a valid or conclusive measure of apes' capacity for ostension.[1]

Introduction

An overarching question in the study of pragmatic communication in non-human primates is whether they have the capacity for ostensive communication. Ostension is, by definition, pragmatic, as it functions based on inferences drawn from the context of the interaction to both imbue and interpret the full meaning of a communicative display. The ostensive model of communication sets a high bar in terms of cognitive complexity; prevailing theories hold that any species that is conclusively shown to successfully produce or comprehend ostensive communication is engaging in inferences about the mental state of the other (Wilson & Sperber, 2002; Csibra & Gergely, 2009; Scott-Phillips, 2015). The ability to interpret ostension also speaks to a cognitive capacity to integrate and discriminate relevant pieces of context and information to rationalize otherwise ambiguous signals, which requires nuanced situational reasoning. These intricate cognitive prerequisites to ostension, and the current paucity of conclusive evidence of ostension in non-human animals, has led some to theorize that humans are uniquely capable of ostension, and that other species may express themselves in flexible and intentional, but distinctly non-Gricean ways (Bar-On, 2013; Scott-Phillips, 2014; Townsend et al., 2017; Heintz & Scott-Phillips, 2022). In fact, some theories suggest that the development of mental state attribution (theory of mind) in humans is driven by the acquisition of language, and is therefore unlikely to be found in non-human species (de

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Villiers & Pyers, 1997; Astington, 2006; Rabkina et al., 2018), which theoretically precludes their capacity for ostension.

The cognitive richness of ostension has inspired a line of comparative research into the evolutionary roots of the ability, including probes into whether it is truly unique to humans. A common form of inquiry into communication in non-human primates has been to compare the performance of preverbal (or linguistically immature) human children with great apes on analogous tasks. Typically, human infants outperform apes in communication comprehension tasks with a human experimenter, such as comprehension of referential pointing (e.g.,Tomasello, Call, & Gluckman, 1997; Hare & Tomasello, 2004; for review, see Tomasello, 2008) or differentiation between communicative motivations (e.g., Herrmann & Tomasello, 2006). Similarly, human infants have been repeatedly shown to understand communicative intention in an information-sharing context (Behne et al., 2005; Gräfenhain et al., 2009; Moore et al., 2013). Tasks which explicitly compare apes' performance in ostensive and non-ostensive conditions, where both displays are referential but only one is addressed to the ape, are few and far between, and have mixed findings: some have found no effect of ostension (Lyn & Savage-Rumbaugh, 2000) and some results suggest that apes do differentiate between these two contexts (Marno et al., 2022). Although many studies have compared apes and children on referential communication tasks, to my knowledge, there is no empirical study which has specifically examined comprehension of communicative intention in both apes and human children using a functionally identical task.

The current study addresses this gap in the empirical literature on ostension in great apes; it was designed to test whether chimpanzees differentiate between ostensive and non-ostensive behaviour to inform their search strategy in a forced-choice task. I designed and conducted this experiment in collaboration with colleagues at the Central European University in Budapest[2], who collected data with 18-month-old human infants using the same paradigm. The definition of comprehension of ostension in this experiment follows relevance theory (Sperber & Wilson, 1986; Wilson & Sperber, 2002): the ostensive display should, by virtue of its communicative intention, trigger in the subject a presumption that the producer's behaviour contains relevant information, which they should use to make rational inferences about the exchange. In the context of this study, I present subjects with a choice between two cups, one of which contains a food reward. I display one cup with ostensive behaviour and interact with the other in a non-ostensive manner. Both displays are designed to enhance interest in and draw the subject's attention to the location, controlling for stimulus enhancement, but only the ostensive display contains a communicative intention, and thus only the ostensive display should trigger rational inferences based on relevance. Given the context of the game – the subject has seen me hide the reward in one cup but has not been able to track which cup it is in – subjects should make the rational inference that I am sharing information about the location of the food reward and should modify their search strategy accordingly. If the subjects are sensitive to whether they are being addressed by my behaviour, they should not presume similar relevance from the non-ostensive display.

Apes have been shown to make inferences about the location of hidden objects in a forced-choice task using various physical cues (Call, 2004; Völter & Call, 2014), logical assumptions (Call, 2006), and even social cues such as eye gaze and manual gestures (Itakura et al., 1999; Peignot & Anderson, 1999; Byrnit, 2004). Given their prowess with physical

cues in similar forced-choice paradigms, we should expect the apes to capitalize on information, if they believe it is available, to inform their searches. Some of the above paradigms showing apes' successful use of social cues have been criticized, because they were conducted with enculturated apes only, and also because the cues may have served only as socially-facilitated stimulus enhancement, and not mechanisms to share information (see Call et al., 2000, Byrnit, 2009). The current experiment is conducted with non-enculturated chimpanzees and juxtaposes ostensive and non-ostensive displays in the same trial, where I interact with both possible food locations, controlling for these two criticisms.

The aim of this experiment is to determine whether chimpanzees can distinguish communicative intention from non-communicative behaviour from a human communicator, and whether their subsequent presumption of relevance guides their search strategy, with the effect of social stimulus enhancement controlled. The prediction is that if chimpanzees are sensitive to ostension, and able to make rational inferences about the location of the food based on their presumption of relevance, their search strategy should be biased toward the ostensively displayed food location.

Methods

Subjects

Subjects for this study consisted of 8 chimpanzees (*Pan troglodytes*) housed at Royal Zoological Society of Scotland (RZSS), Edinburgh Zoo. The initial pool of subjects included 13 chimpanzees; 5 of these subjects were not included in the experimental phase due to failure to meet the minimum criteria during the training phase (*N*=4) or subsequent loss of interest (*N*=1). Subjects varied in rearing history and were classified as follows: *wild* (subject born and reared throughout infancy in a wild environment); *hand-reared* (subject was reared exclusively by or had extensive contact with human caregivers); and *parent* (subject was reared in captivity by parent and other conspecific individuals, or parent-reared with minimal assistance from human caregivers). Of the final group of 8 subjects, 7 chimpanzees had past experience with both forced-choice tasks using pointing to indicate selection and tasks involving rewards concealed by cups, but none of the subjects had prior experience with the specific materials or the specific communicative behaviours used in this design. One adult female subject's history was unknown regarding experience with research of this nature (see Table 2.1)[3].

Table 2.1 Subject Demographic Information

Name	Age	Sex	Rearing History	Prior Task Experience	Participation
Lucy	42	F	Parent	Yes	completed study
Kilimi	26	F	Parent	Yes	completed study
Tupelo	26	F	Parent	Unknown	completed study
David	44	M	Parent	Yes	completed study
Louis	42	M	Wild	Yes	completed study
Qafzeh	27	M	Parent	Yes	completed study
Frek	25	M	Parent	Yes	completed study
Velu	4	M	Parent	Yes	completed study
Eva	38	F	Parent	Yes	did not pass training phase B
Sophie	37	F	Hand-reared	Yes	did not participate in experimental phases
Edith	24	F	Parent	Yes	did not pass training phase B
Paul	26	M	Parent	Yes	did not pass training phase A

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[3] This study was conducted with ethical approval from the University of St. Andrews School of Psychology and Neuroscience Ethics Committee (see **Appendix G**).

| **Liberius** | 20 | M | Parent | | Yes | | did not pass training phase B |

Materials

I conducted the experiment with all subjects, after a period of familiarization with each subject. Testing occurred in the Budongo Research Unit (BRU) – a space which consists of designated research rooms adjacent to the chimpanzee's indoor enclosure (see **Appendix B**). I tested subjects individually, but individuals were not separated from their groupmates or denied access to their enclosure during testing, and it was therefore possible for other individuals to observe or interfere during trials. I did not proceed with testing until the focal individual was not interacting with or distracted by conspecifics, and I halted and restarted trials if interrupted by a conspecific.

Subjects participated in the experiment by approaching and sitting opposite me, separated by a polycarbonate window panel (positioned at panel 6, see "panel 6" in the BRU, **Appendix B**). The experimental set-up consisted of a polycarbonate shelf suspended from the panel on the experimenter's side by two plastic cords tied to an acrylic rope and secured to the top edge of the window. I used plastic capsules taken from the inside of Kinder Eggs™ (hereafter, "eggs"), lined with duct tape to ensure opacity and adhered to aluminium jar lids to ensure that they would stay upright when opened, to conceal high-value food rewards (this container was modelled after the container used in the design for infant humans). I placed a rectangular polycarbonate slider on top of the shelf to slide the eggs back and forth, and I used a polycarbonate feeding tube, located beneath the shelf, to pass food rewards to the subject. I placed a carboard occluder at my feet, beneath the feeding tube, to conceal the eggs during portions of the baiting. Subjects could indicate their choices by pointing through one of three equidistant holes (3cm diameter) spaced horizontally along the bottom third of the polycarbonate panel (see Figure 2.1). All trials were videotaped from my perspective, with the camera positioned to look over my shoulder.
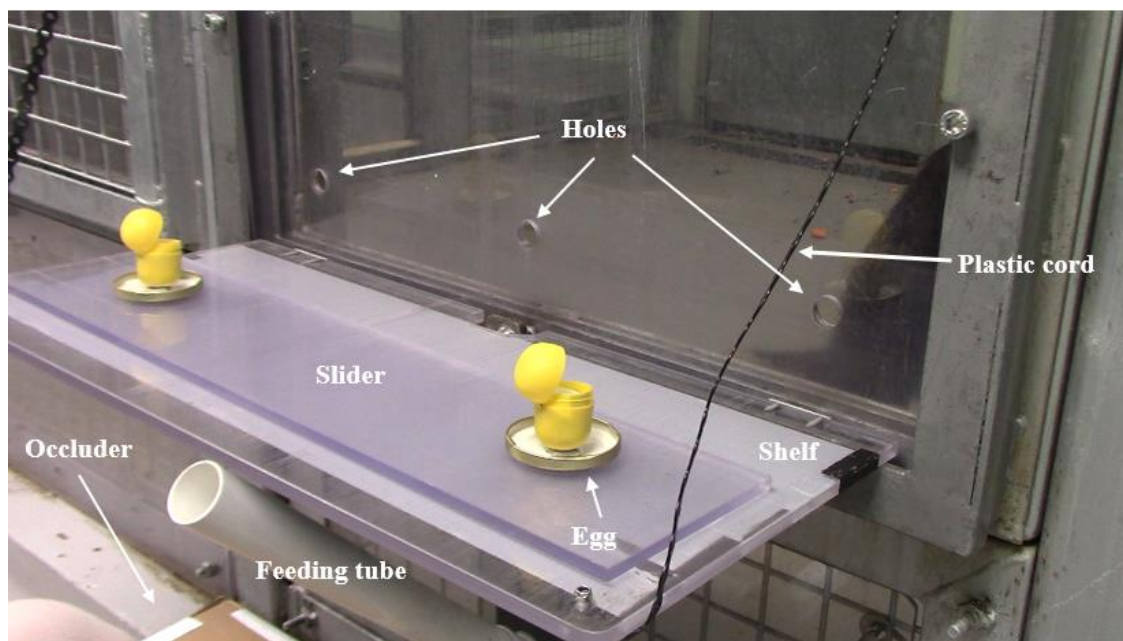
Figure 2.1 Image of experimental set-up, with elements of the apparatus and testing environment labelled

Procedure

The experiment included a training stage with two phases, followed by an experimental stage with three phases (two critical conditions and a control). The design was within-subjects, such that all subjects participated in all conditions, though the order of the two of critical conditions was counterbalanced by subject. I administered the control condition after both critical conditions for all subjects, to prioritize the experimental conditions in earlier trials, where the effect of habituation from the indiscriminately rewarded structure of testing might be less pronounced. All trials required a choice between two eggs, and I always counterbalanced the baiting location and/or the order in which the eggs were manipulated in a randomized order.

I administered testing over five blocks of twelve trials each: one for each of the two training stages and one for each of the three experimental phases. Subjects could complete a maximum of twelve trials per day, and blocks could be completed over multiple days if the subject did not complete the full twelve trials in one sitting. In the event that a subject failed to meet the criteria to pass one of the training stages, I administered additional blocks of twelve trials in the same stage and advanced the subject to the next phase if and when they passed the training criteria.

Training Stage

Training Phase A

Training phase A was intended to verify subjects' understanding of the forced-choice nature of the task and to ensure that all subjects were comfortable with pointing to indicate a choice. I placed two eggs, empty, with lids open, on the on the slider, in front of the left and right holes, respectively. I ensured the subject's fingers were not already inserted into the choice holes and then baited one of the two eggs with a food reward. I tapped each egg twice against the slider to simulate later conditions where each egg would be manipulated in turn, and then slid the eggs toward the subject until the slider made contact with the polycarbonate window. I recorded the first unambiguous selection after the slider made contact with the window; either the subject had already inserted a finger through the corresponding hole before the slider moved forward and kept it in place, or they did so after the slider made contact with the window. If the subject chose the baited location, they received the food reward through the feeding tube.

In the event of an ambiguous choice, such as fingers inserted through two different holes simultaneously, fingers inserted into the centre hole, or no choice at all, I moved the slider backward and immediately slid it forward again to allow a second attempt. If the subject made two ambiguous choices in a row, I ended the trial. I required subjects to make six unambiguous choices in a row within a twelve-trial block in order to pass this phase. One subject did not pass this criterion and was not included in the final sample.

Training Phase B

Training phase B was intended to ensure that subjects were capable of tracking the location of a hidden food reward from the point of baiting until they were offered a choice. Training phase B proceeded in the same manner as the training phase A, but following baiting, I closed each egg in turn, obscuring the food reward but allowing the subject to track or remember its location. I then offered subjects a choice, as in training phase A, with the same criteria for

unambiguous choices. I required subjects to choose the baited location on ten out of twelve trials in order to advance to the experimental phase. For subjects who failed this criterion, I administered additional blocks of twelve trials within this phase as many times as they continued to show interest, or until they passed the criterion. Three subjects did not pass this criterion due to a persistently side-biased search strategy and were not included in the final sample.

Experimental Stage

I followed the same procedure for baiting in all three experimental phases – I placed the eggs aligned front and back, perpendicular to myself and to the subject, in front of the centre hole. I then baited the front egg and closed both eggs, first the front egg, then the back, empty egg. I then used both hands to scoop the eggs toward myself, off the shelf and underneath the occluder, I shuffled them for two seconds. Simultaneously, I switched the empty egg for a hidden, baited egg, out of view of the chimpanzee. Thus, the chimpanzee only saw one food reward, and presumably believed that there was only one correct food location, but the trials were indiscriminately rewarded, to avoid any learning effect. I then brought the two baited eggs back up to the shelf and aligned them in front of the left and right holes, respectively.

I then "searched" each egg, before displaying each egg for four seconds, one with ostensive behaviour, and one with non-ostensive behaviour, using different sets of behaviour according to condition (see Table 2.2). After each display, I replaced the egg on the slider in front of its respective hole. After both displays, I offered the subject a choice, with the same criteria for unambiguous selection as in the training phases. I gave the subject the food reward from whichever egg they indicated and did not show them that the other egg also contained a food reward. The experimental conditions were as follows:

Baby-Same: This condition was intended to administer a comparable protocol to that given to 18-month-old infants by our colleagues at Central European University. The search behaviour (visually gazing at the egg), ostensive display, and non-ostensive display were based on infant-directed cues such as smiling, "motherese" tone of voice, and linguistic verbal phrases (see Table 2.2).

Chimp-Friendly: This condition was intended to replicate the design of the experiment delivered in infants, but modified to replace the search and display behaviours with actions found in the natural foraging and attention-getting behavioural repertoires observed in chimpanzees (Hobaiter & Byrne, 2011) (see Table 2.2).

Table 2.2 Sets of behaviour used in each type of display across both critical conditions

Baby-Same		**Chimp-Friendly**	
Search: gaze at egg		Search: smell egg	
ostensive	*non-ostensive*	*ostensive*	*non-ostensive*
gaze at subject	gaze at egg only	gaze at subject	gaze at egg only
smile at subject	smile at egg only	attempt eye contact	no eye contact
attempt eye contact	no eye contact	extend egg toward subject	keep egg close to own body
point at egg	hold egg in both hands	call subject's name	no use of subject's name
verbal phrase using "motherese" tone*	verbal phrase using "neutral" tone**	shake table cord (audible sound)	cleaning motion against arm (audible sound)
call subject's name	no use of subject's name		

Control: The purpose of this condition was to examine whether factors other than the two displays of the eggs were influencing subjects' search strategy, such as incidental cues from the experimenter, or specific features of the apparatus design and location. After I shuffled and swapped the empty egg for the hidden, baited egg, I placed the two baited eggs in front of the left and right holes, respectively. I then immediately offered the subject a choice, with no communicative displays for either egg.

Scoring and Analyses

Across all experimental phases, I scored the subject's first unambiguous choice from live coding and confirmed them using video recordings. In the baby-same and chimp-friendly conditions, I scored choices for two binomial measures: search pattern (0 = left, 1 = right, from my perspective), and bias toward ostension (0 = choice to the non-ostensively displayed side, 1= choice to the ostensively displayed side). For the control condition, I scored only search pattern. To assess group-level performance between and within experimental phases, I aggregated the data by subject. I examined bias toward ostension by taking the mean number of choices to the ostensively displayed side for each subject, such that each subject's pattern of choices could vary between 0 and 1. I assessed search pattern by taking the count of all choices to the right for each subject, and then reverse-coding those subjects with a count of <6 ($N_{reversed} = 12 -$ raw count), such that the count per subject represents the number of choices to the more-preferred side (if any), regardless of which side the subject chose more often.

An additional coder, naïve to the empirical questions and predictions of this study, scored choices to the left or right for 10% of trials. I assessed interobserver reliability using Cohen's kappa and found extremely high agreement between the two observers ($K=1$, $N=38$, $p<0.001$).

Ostension bias was normally distributed in both the baby-same and the chimp-friendly conditions, according to Shapiro-Wilk tests of normality ($p=0.324$ and $p=0.156$, respectively). I assessed group-level bias toward ostension within each critical condition using one-sample t-tests with a criterion p-value of $p<0.05$ and a 95% confidence interval, to evaluate the pattern of choices in each condition compared to chance (50%). I compared individual bias toward ostension within each condition to chance (50%) using binomial exact tests, with a p-value criterion of $p<0.05$ and a 95% confidence interval. The difference in ostension bias between the two critical conditions was not normally distributed according to a Shapiro-Wilk test ($p=0.032$). I assessed the difference in bias toward ostension between critical conditions using a paired Wilcoxon signed rank test.

The distribution of choices to a single side in the control phase was not normally distributed (Shapiro-Wilk: $p=0.010$). I therefore compared search pattern in each experimental phase to chance (50% of choices to each side) using one-sample exact Wilcoxon tests. I then compared search pattern across all three experimental phases using Friedman's ANOVA and between phases using pairwise exact Wilcoxon tests. I compared individual search pattern within each condition to chance using binomial exact tests, with a p-value criterion of $p<0.05$

and a 95% confidence interval. All means are displayed with standard error. All medians are displayed with interquartile range (*IQR*). I conducted all statistical analyses using RStudio version 4.2.1.

Results

Bias Toward Ostension

Subjects showed no bias toward ostension in either the baby-same condition (*mean*=0.531 ± 0.027, *t*=1.158, *df*=7, *p*=0.285), or the chimp-friendly condition (*mean* =0.510 ± 0.029, *t*=0.357, *df*=7, *p*=0.732); subjects' choices did not differ significantly from chance. There was also no difference in ostension bias between the two critical conditions (*W*=7, *N*=8, *p*=0.584) (see Figure 2.2). No individual's bias toward ostension differed from chance (see **Appendix C**).
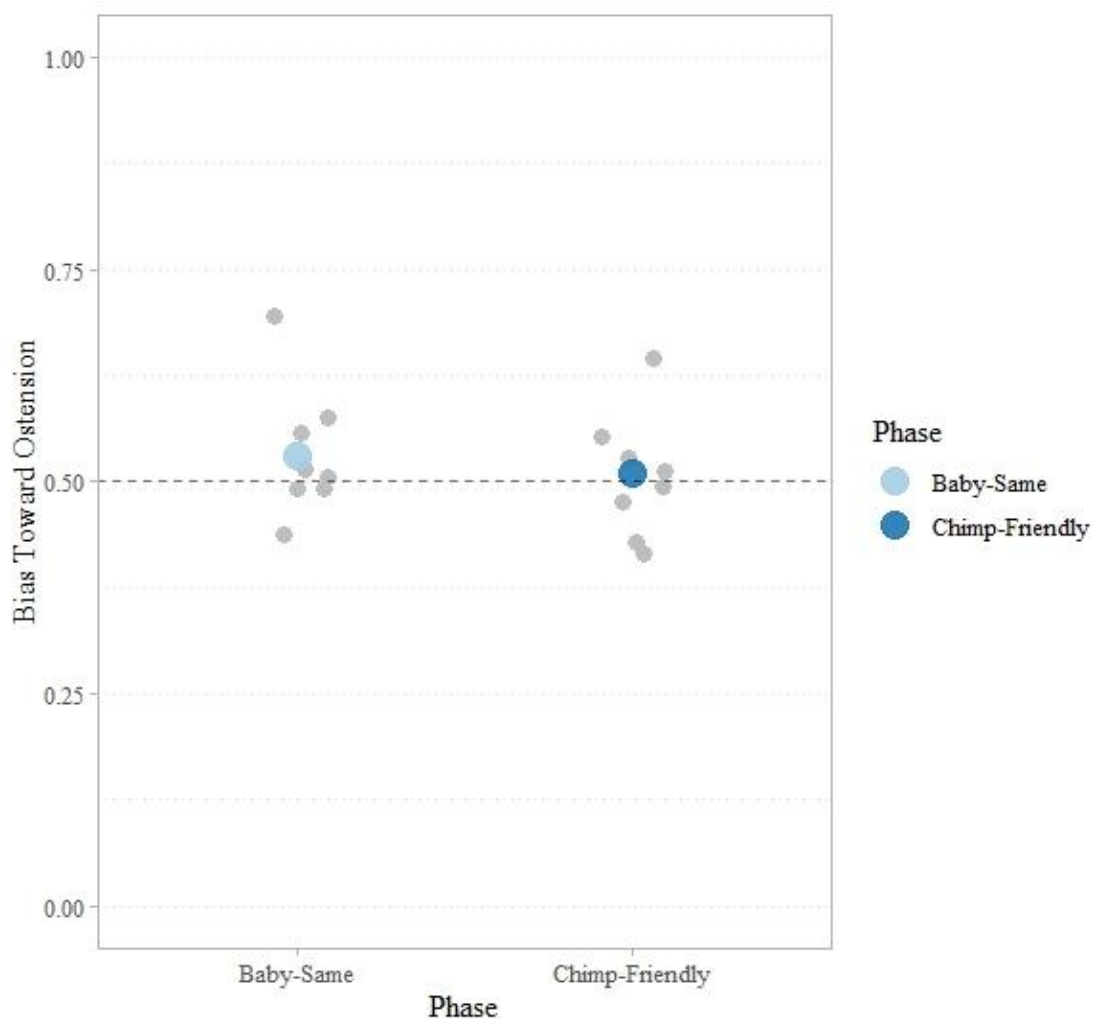
Figure 2.2 Group mean bias toward ostension (individual means shown in grey) across both critical experimental conditions. The dashed line represents 50% chance, or lack of bias toward either the ostensive or the non-ostensive display.

Search Pattern

Analysis of search pattern in the control phase revealed a group-level side-biased search strategy, with a median of 12 (out of 12) choices to a single side (*IQR*=0.25). This pattern was significantly different from chance (*W*=36, *N*=8, *p*=0.010). There was a non-significant trend toward a difference in search strategy between experimental conditions (*Friedman's* χ^2= 5.25, *df* = 2, *p*=0.072).
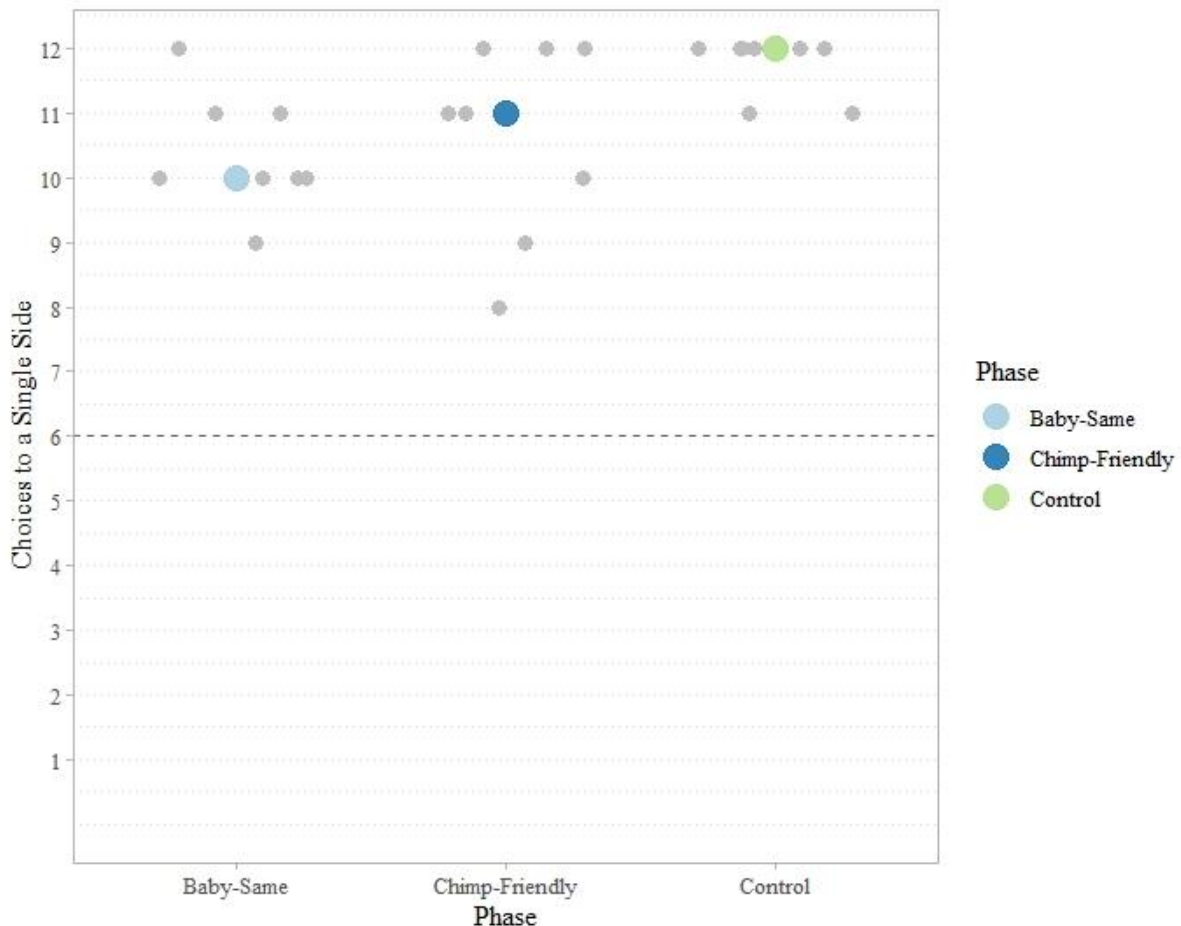
Figure 2.3 Group median choices to a single side across three experimental phases. The dashed line indicates chance performance (equal choices to the left and right). Individual counts of choices to a single side are shown in grey.

There was a group-level side-biased search strategy in both critical experimental conditions, similar to that found in the control condition; the group median choices were significantly different from chance performance of 6 choices per side (baby-same: *median*=10, *IQR*=1, *W*=36, *N*=8, *p*=0.013; chimp-friendly: *median*=11, *IQR*=2.25, *W*=36, *N*=8, *p*=0.014) (see Figure 2.3). When the data is broken down by subject, this side-biased search strategy was apparent in all eight chimpanzees, with all but two subjects consistently choosing their apparent preferred side at a rate significantly above chance in all three experimental conditions (see Figure 2.4, see **Appendix C**).
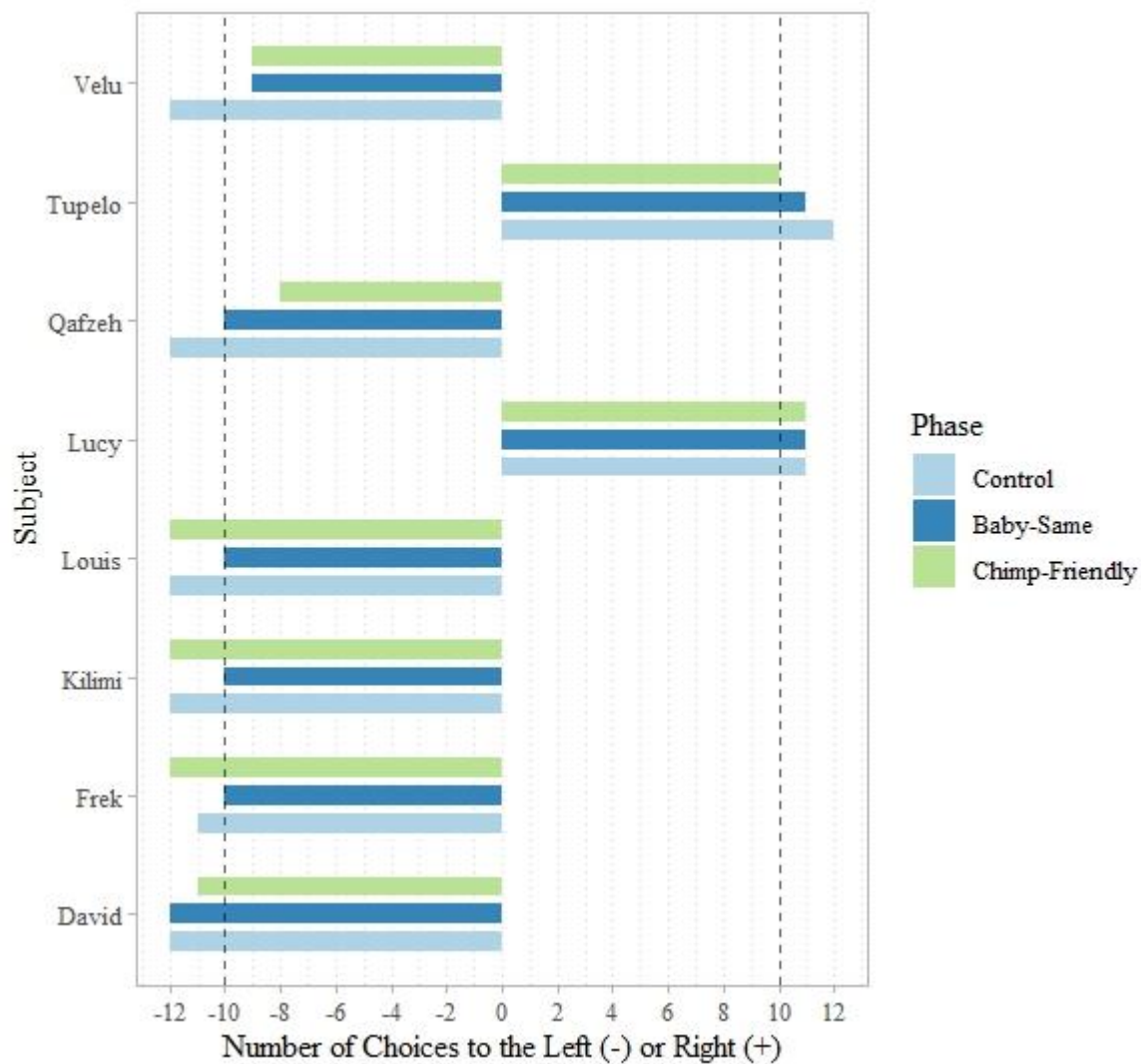
Figure 2.4 Visualization of individual subjects' search strategy over twelve trials for each experimental phase, with number of choices to the left (from the experimenter's perspective) represented as negative values and number of choices to the right represented as positive values. Subjects favouring one side at a rate of 10 trials or more per phase (see dashed lines) are choosing their preferred side significantly above chance. *exact binomial tests (see **Appendix C**).*

Discussion

This study did not find evidence that chimpanzees are sensitive to the relevant nature of ostensive behaviour – that is, subjects did not show any indication that they interpreted information about the location of the food reward based on my ostensive behaviour, and they did not modify their search strategy based on the ostensive display. Rather, all subjects showed a distinctly side-biased search pattern in all three experimental phases, persistently selecting the egg on their preferred side and choosing at chance between the ostensive and

non-ostensively displayed options. This null result should be interpreted with caution, however, given several limitations and theoretical weaknesses in the design of this study.

This null finding is in line with an extensive list of studies in which apes fail to acquire information about the location of hidden food or objects by following an informational human pointing gesture or by inferring information from a human demonstration (see reviews by Krause, 1997; Tomasello, 2008; Moore, 2013; and der Goot et al., 2014). While not all of these studies asked questions relating to specifically to comprehension of ostension, they shared the requirement that the subject select a location or option based on the informative behaviour of a human experimenter, interpreting signals derived from the human communicative repertoire (e.g., pointing, waving, linguistic utterances). Leavens et al. (2019) eloquently make the argument that these designs share a common methodological weakness: they all use gestures "culturally situated" in human culture. Enculturated and cross-fostered apes tend to outperform their captive, but conspecific-reared peers in comprehending and producing points (Call & Tomasello, 1994; Leavens, 2005; Lyn et al., 2014), which supports the idea that extensive exposure to human gestures and communication styles throughout ontogenetic development establishes some of the common ground necessary for the primate subject to assume that pointing gestures are cooperative and informative. Failure in these tasks, then, is not necessarily due to primates' inability to use communication to convey or receive information, but to a lack of mutually held expectations about the purposes of specific signals. Put more simply, apes may fail in these tasks because the informational signals are too specific to humans, and the apes do not have the appropriate usage experience through which to interpret them. The body of work finding overall failure of apes to use informative human signals to choose between options should therefore be interpreted with caution, since it shares a systematic weakness in assuming that the same signals which are successfully interpreted by humans will be correctly interpreted by apes. The current study shares this methodological flaw, particularly in the baby-same condition, and this may account in part for the null finding.

The limitation of human-derived display signals is particularly relevant to the baby-same condition of the current study, which directly matched the signals used for infants, but I argue that the theoretical flaw in this design runs deeper than just the exact suite of behavioural signals in the design. The chimp-friendly condition of this study was intended to help mitigate the interspecific communication concerns, by using signals familiar from the natural

repertoire of chimpanzees, but it may have fallen into the same trap as pointing and infant-oriented paradigms in the sense that the primate subject still lacks the common ground to interpret the human signal as informational. For example, the ostensive, attention-getting, chimp-friendly signal - shaking the cord of the table – resembles branch-shaking and stick-shaking behaviours used between chimpanzee conspecifics, but the nature of the gesture in the method of this study was declarative (i.e., sharing information about the location of the food), and not imperative. Although apes have been shown to use gestures intentionally and referentially, both in captivity and in the wild (e.g., reviews by Pika & Mitani, 2006; Gómez, 2007; Douglas & Moscovice, 2015; Fröhlich et al., 2019), they seldom, if ever, use these gestures declaratively (although a few accounts of enculturated apes and one anecdote of wild bonobos (*Pan paniscus)* suggest that apes may, on rare occasions, use gestures declaratively, see Leavens et al., 2004; Veà & Sabater-Pi, 1998). As with human-derived informational gestures, primates may also lack the common ground with humans to recognize the use of primate-derived gestures when they are performed declaratively by a human experimenter, either because the gestures are non-sensical when performed by a human or because the primate subject does not relate the use of attention-getters and other communicative signals to declarative information. Thus, although the ostensive displays in either the baby-same or the chimp-friendly phases of the current study may have directed the attention of the subjects, and may even have registered as efforts to communicate with the subjects, the declarative message could have been lost, due to a lack of mutual expectations about information-sharing gestures. Hopkins et al. (2013) discuss the importance of methodology in this context – they note that chimpanzees appeared to regard human informative gestures as relevant and correctly used them to infer a desired location in the context of a task which was more ecologically relevant to chimpanzees: the informative point was an imperative request to exchange a specific one of several objects, rather than a declarative point about the contents of a location of a hidden object. The current finding fits in to the discussion of methodological validity; there are confounds in the human-oriented task and displays in this design that limited its ability to investigate inferential interpretation of ostension in non-human primates.

Regarding confounds within the current task, the arrangement of the two displays in the same trial may have increased task confusion, leading to a side-biased search strategy. This design offered the opportunity to assess a very fine-tuned distinction between ostensive and non-ostensive behaviour, by juxtaposing two displays which theoretically both inform the same

search decision. By placing the two displays on the same trial, however, it is possible that they were not regarded as separate events, but rather as one long manipulation of the apparatus, with each display therefore confounding the other. In this interpretation, the experimenter's behaviour may have been perceived as communicating about both eggs, or neither egg, rather than communicating about one egg only. This increases the demand that the subject comprehend not just the communicative nature of the display, but the actual meaning of the message. This paradigm was not intended to measure whether apes can receive actual semantic messages (i.e., "the food is here") from humans – the research question under investigation was whether apes are sensitive to the ostensive nature of communication and whether they can use that distinction to interpret information that follows. Although it seems logical, in studies of humans, that the most straightforward way to diagnose comprehension of communicative intention is to measure whether the intended message was received, sensitivity to ostension and comprehension of semantic meaning are separate demands. This limitation could be addressed by modifying the experimental protocol such that there is only one display per trial – one egg is manipulated, either ostensively or non-ostensively, and the other egg is not, with a third condition to control for simple stimulus enhancement. I argue, however, that such a modification would be an unproductive path forward, unless the above and following theoretical and empirical weaknesses in this design are also addressed.

A related limitation in this experimental protocol is that the subject's role was a relatively passive one. It may have appeared to them that I persistently manipulated the apparatus with no salient goal and then they received a grape reward for pointing, and they may not have regarded the display as pertinent to their search strategy. As soon as the eggs disappeared from view and the subject could no longer visually track the reward, the object of the game may not have been clear to them, especially if, as discussed above, they are not prepared to receive declarative information. This is particularly true in terms of a learning effect – the trials were indiscriminately rewarded, and this may have encouraged even less attention to the displays over time. A more engaging task, in which the subject needs to acquire some information from the experimenter before completing a task themselves, such as a puzzle or foraging task, may have encouraged more attention to the communicative displays. A task such as the exchange protocol used by (Hopkins et al., 2013), may be more appropriate, if I were to persist with this line of investigation using informational displays to inform primate's choosing behaviour. An alternative criticism of the experimenter/subject roles in this task is

that the entire experimental set-up could be viewed as ostensive – the experimenter is performing actions for no other apparent reason than for the benefit of the subject, whether the actions are ostensive or not, and a subject sensitive to ostension may perceive the entire interaction as addressed to them, given the highly artificial conditions of the testing environment. This criticism applies in both the human infant and non-human primate iterations of this experimental paradigm and could equally account for the floor effect of bias toward ostension. It is worth noting that 18-month-old human infants also performed at chance in this task (Scott-Phillips, unpublished data)[4], suggesting that the weaknesses in the design were not limited to the primate model.

A final criticism of this design, which pertains to the validity of the critical difference between the ostensive and non-ostensive displays, is that the displays differ not only in whether they are addressed to the subject, but also in their emotional valence. The ostensive display, with the "motherese" style of speech and exclamatory tone, has more positive valence than the calmer and more serious non-ostensive display, and these actions could therefore have engendered different emotional states in the subject, regardless of their comprehension of the nature of the communication. This emotional state could have guided their reactions as easily as their sensitivity (or otherwise) to ostension, and even if the results has shown a significant bias toward the ostensively displayed side, this paradigm would be unable to determine whether the result was due to a different in communication cognition or a difference in emotional state. A more effective paradigm investigating sensitivity to ostension should control for factors such as emotional valence by either including a control condition which is not communicative but is positively charged, or by introducing multiple ostensive displays with varying emotional valence, to tease out the effects of emotion associated with communication.

The results of this experiment, and my subsequent review of the invalidity of the stimuli and response variables in this design, lead me to the opinion that this and similar paradigms are not an effective or illuminating method to study sensitivity to ostension in non-human animals. I believe that empirical approaches which centre human-derived communicative behaviours and demand that subjects report their direct understanding of the communicated message through their choices or successes in a task are not appropriate or falsifiable

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[4] Data presented by Thom Scott-Phillips during quarterly meetings of the collaborators on ERC Synergy Grant ERC_609819 [SOMICS].

measures of the capacity for ostension, because they do not account for the many other factors that could contribute to a null result. In subsequent experiments, I was inspired by methodology used in paradigms assessing sensitivity to ostension in canines (e.g., Topál et al., 2014;Tauzin et al., 2015a; Tauzin et al., 2015b), which adopt a strategy derived from the theory of natural pedagogy (Csibra & Gergely, 2009) and assess sensitivity to ostension by measuring changes borne out in the behaviour of the canine subjects. This includes changes to the natural, untrained behaviours of the subjects, such as looking behaviour, and changes to existing biases, such as perseverance biases. I focused my forthcoming work on assessing the capacity for ostension using designs which measure changes in untrained and unsolicited behaviours from the subjects, and which remove the task demand that the subject interpret a semantic message. I also ensured that these paradigms addressed the confounding questions of attention, stimulus enhancement, and emotional valence in communicative displays. Finally, I designed some tasks with a more active role for the subject, which allowed me to both mitigate the lack of engagement due to subject passivity and to assess whether the subjects do, indeed, view me as an agent that can produce and receive communication, a prerequisite for the comprehension of ostension. This reconsideration of methodology is expanded in a theoretical review and analysis of models of animal communication in Chapter 3 and in empirical work detailed in Chapters 4, 5, and 6.

Chapter 3 Inferential Communication: Bridging the Gap Between Intentional and Ostensive Communication in Non-Human Primates

Summary

The following chapter is a review and analysis of the gap in both the theoretical conceptualization of and the empirical frameworks investigating flexible, goal-oriented, context-dependent communication in non-human animals. I published this paper with my supervisor (Warren & Call, 2022) as part of a special issue of *Frontiers in Psychology*, entitled "The Quest for Symbolic Communication in Non-Human Animals."[5] Following my analysis of the theoretical and practical limitations of the previous study (Chapter 2), particularly the challenges associated with investigating animal cognition using experimental models designed for humans, I took a deep dive into the existing models of animal communication and worked to conceive a bottom-up conceptual and empirical approach to communication cognition without the limiting constraints and prerequisites of ostension as it is understood in humans. At the same time, I sought to go beyond the restricted view of animal communication as intentional, but absent any engagement with mental states or situational interpretation of signals. In addition to a review of existing models of animal communication, this paper develops the following concepts from a theoretical and practical point of view: pragmatic inference and its role in communication; flexible interpretation of others' goals and its bearing on interpretation of communication; the decoupling of informative and communicative intention in social exchanges; and empirical approaches to the study of inferential communication.

Abstract

Communication, when defined as an act intended to affect the psychological state of another individual, demands the use of inference. Either the signaller, the recipient, or both must make leaps of understanding which surpass the semantic information available and draw from pragmatic clues to fully imbue and interpret meaning. While research into human communication and the evolution of language has long been comfortable with mentalistic interpretations of communicative exchanges, including rich attributions of mental state, research into animal communication has balked at theoretical models which describe mentalized cognitive mechanisms. We submit a new theoretical perspective on animal communication: the model of inferential communication. For use when existing proximate models of animal communication are not sufficient to fully explain the complex, flexible, and intentional communication documented in certain species, specifically non-human primates, we present our model as a bridge between shallower, less cognitive descriptions of communicative behaviour and the perhaps otherwise inaccessible mentalistic interpretations of communication found in theoretical considerations of human language. Inferential communication is a framework that builds on existing evidence of referentiality, intentionality, and social inference in primates. It allows that they might be capable of applying social inferences to a communicative setting, which could explain some of the cognitive processes that enable the complexity and flexibility of primate communication systems. While historical models of animal communication focus on the means-ends process

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of behaviour and apparent cognitive outcomes, inferential communication invites consideration of the mentalistic processes that must underlie those outcomes. We propose a mentalized approach to questions, investigations, and interpretations of non-human primate communication. We include an overview of both ultimate and proximate models of animal communication, which contextualize the role and utility of our inferential communication model, and provide a detailed breakdown of the possible levels of cognitive complexity which could be investigated using this framework. Finally, we present some possible applications of inferential communication in the field of non-human primate communication and highlight the role it could play in advancing progress toward an increasingly precise understanding of the cognitive capabilities of our closest living relatives.

1. Introduction

Communication modifies the behaviour of others by altering the psychological state of the recipient. Unlike instrumental actions, which bypass the recipient's psychological states and act directly on their behaviour, communicative acts affect the perception, attention and/or cognition of recipients, and, if successful, subsequently provoke the desired behaviour. Consider, for example, an infant chimpanzee who, while clinging to their mother, begins to nurse. The infant is engaged in an instrumental action with a direct effect on the mother's body, without engagement with the mother's psychological state. Although the mother could choose to disrupt the infant's feeding behaviour if she did not desire that interaction, the feeding interaction itself is instrumental, not communicative. Conversely, an infant chimpanzee who reaches their hand toward their mother's back, a ritualized gesture which requests carrying (Hobaiter & Byrne, 2014), is altering the mental state of the mother, who may react to her perception and cognitive processing of this event by lifting the infant onto her back and performing the desired carrying behaviour. Although the ultimate outcomes of the two interactions are similar – the infant's physical needs are met – the proximate mechanisms that permitted these outcomes are fundamentally different. The proximate mechanisms of communication, the alteration of psychological states to influence behaviour, are an exceptional lens through which we can probe the levels of cognitive engagement involved in different communication systems.

Psychological states play a central role in all forms of communication, from the wing spots of a butterfly to the courtship display of a gull to linguistic exchanges between humans. These systems of communication differ, however, in their origins and, more importantly for our purposes here, in fixedness of the signals and in how likely they trigger certain responses in the audience that receive them. In cases where invariable signals precede invariable responses, there is little room for cognition. Therefore, dispensing of the cognitive 'waystation' in such cases does not represent a substantial loss, and communication can be viewed as signals or actions used to alter behaviour. The breadth of communicative behaviour, however, cannot be fully encompassed by fixed signals with involuntary responses.

Bypassing cognition becomes more difficult when the signals and responses are not fixed, but rather show some degree of variability. Flexibility in communication was first recognized by zoosemioticians studying the meaning of animal signals (e.g. Marler, 1961; Plooij & Lock, 1978) and later by researchers interested in intentional and goal-directed communication (e.g. Byrne et al., 2017; Tomasello et al., 1985). Both the early "signal meaning" approaches and the later intentional/goal-directed approaches to communication address cognitive aspects, but we will argue that neither of them is sufficient to fully explore how animals might use psychological states, and particularly some forms of inference about mental states, to

communicate. In fact, some recent contributions that have embraced cognitive models of communication (e.g., Townsend et al., 2017) have flatly rejected mentalizing at any level and instead focus on superficial features of communication that denote flexible cognition. We think that this is a regressive mistake. The Gricean approach (Grice, 1957; Grice, 1969), which theorises a high level of cognitive complexity, including pragmatic meaning, in communicative exchanges, is difficult to implement in investigations and interpretations of animal communication. The central idea that mentalizing plays a role in animal communication, however, deserves careful consideration.

One problem with completely rejecting mentalizing in animal communication, particularly if one is interested in the flexibility of a communicative system, is that mentalizing unlocks an unprecedented level of flexibility in human communication. Since many cognitive approaches to animal communication have used human communication as a point of comparison, particularly in considerations of the evolutionary origins of human language (e.g., Hewes et al., 1992; Scott-Phillips, 2015; Zuberbühler, 2005), it is at the very least questionable to *a priori* discard mentalizing. Although documenting flexibility in animal communication by means of behavioural indicators such as means-ends dissociations, contextual variation in signal use, and audience effects is a necessary first step (e.g., Tomasello & Zuberbühler, 2002;Tomasello, 2009 for review), such indicators explain neither the origin nor the psychological underpinnings of flexible responses. Producing a descriptive list of behavioural indicators of flexibility (goal-directedness) without digging deeper into the psychological process that give rise to those responses seems a missed opportunity. The problem is further compounded by the fact that referential and intentional communication are often used to explain language evolution (e.g., Arbib et al., 2008), but language is a system with mentalizing at its core (Grice, 1957;Grice, 1969; Wilson & Sperber, 2002). Without postulating some ability to make inferences about mental state to some forms of animal communication, the leap from animal to human communication, and language in particular, might be too great to be realistic. If the cognitive complexity of human communication is the measuring stick against which animal systems of communication are compared, at least in investigations of the evolutionary origins of language, then there exists a gap between the complexity of communicative behaviour explained by the intentional model of communication and the ostensive-inferential models of human communication whose potential application has been discussed in certain animals, such as non-human primates (hereafter, "primates").

In this article we propose a solution to this gap in current models' explanatory power, for use in situations where the communicative behaviour of a species or taxa involves an apparent level of flexibility and pragmatism not fully explained by existing models. We would like to introduce a model of communication – "inferential communication" – which we will distinguish from the model of intentional communication (e.g., Woodruff & Premack, 1979) and differentiate from other descriptions of inferential communication discussed by Fischer (2013) and Fitch (2015), as well as those posited in developmental literature and studies of linguistics (e.g., Sperber & Wilson, 1986). Our model is not intended encompass the same scope as global models of animal communication with ultimate explanations for communicative behaviour. We submit inferential communication as a proximate model of communication which elaborates on ultimate explanations of communicative behaviour by outlining some of the cognitive mechanisms that may operate within these ultimate models. As we hope will become apparent, our proposal differs from cognitive models of animal communication that incorporate inferential processes on the one hand, and human ostensive communication on the other, along three main dimensions: the nature of the inference, the

type of pragmatics involved and the role of informative intentions. We will combine the comparative research that has been accumulated in the last three decades on referential and intentional communication with data on social cognition and inferential reasoning to establish the theoretical foundations for our perspective on inferential communication. Thus, one of our key proposals is that mental state attribution, rather than being a problem, it is part of the solution. Together with inferential reasoning, it constitutes the cognitive substrate of flexible communication.

Our paper is organized as follows. First, we will summarize the traditional approaches to animal communication, in order of increasing engagement with cognition, and provide the theoretical background to contextualize the model we now propose. Second, we will outline the model of inferential communication, specifically with respect to primates, distinguishing our proposal from previous characterizations of inference in communication. Third, we will delineate the cognitive skills and mechanisms required for each increasingly mentalized level of complexity within our model. Fourth, we will shed light on the applications of inferential communication, from both a theoretical and experimental perspective, and explain the breadth of taxa to which it could potentially be applied. Finally, we will place inferential communication into the broader field of theoretical approaches to primate communication.

2. From Signals to Intentional Gestures

2.1. Manipulation Model

To appreciate the theoretical justification for inferential communication, it is critical to review both the tenets of ultimate approaches to animal communication and the questions they leave unanswered. The earliest ethological models of animal communication, including non-human primate communication, were founded in behaviour, not cognition (see Table 3.1). Building on the work of Tinbergen (1952) and Lorenz (1966), who created the foundation for phylogenetic preservation of evolutionarily successful behaviours, Dawkins and Krebs (1978, 1984) asserted that animal systems of communication are the result of repeated, non-communicative instrumental actions that become phylogenetically ritualized to prompt certain behavioural responses in others. Just as instrumental actions affect the environment to produce a certain result, communicative signals act on others to induce certain behaviours. If successful, the signaller will have incurred benefit as a result of the exchange, and thus the signal persists as a function of evolutionary fitness. This non-mentalized, behaviour-centric approach is upheld in some modern work (e.g., Owren et al., 2010), where animal communication is described as an effort to influence the behaviour of another and is placed in the shared evolutionary timeline of living primate species, including humans, as a necessary but distant step in the evolution of human language.

Table 3.1 Ethological models of communication including the origin and signal-referent relation as well as their key cognitive concepts.

Model	Sub-Discipline	Signal Origin	Signal-Referent Relation	Key Cognitive Concepts
Manipulation	Behavioural Ecology	innate	fixed	n/a

Information	Zoosemiotics	innate/learned	flexible	semantic signal encoding and decoding functional reference

If we apply this model to an example of a communicative interaction between two primates, the ritualized format of the exchange becomes clearer. In this example, one primate, Cindy wishes to be groomed by another primate, Louis. Accordingly, Cindy moves toward Louis and presents her shoulder, a behavioural pattern known to culminate in the receipt of grooming (Hobaiter & Byrne, 2014). Louis grooms Cindy's shoulder, and Cindy therefore receives fitness benefits associated with grooming. Viewing this exchange through the lens of communication as manipulation, Cindy has engaged in a ritualized action which likely developed from the necessary instrumental actions associated with grooming, i.e., moving the body part close enough to allow grooming to occur. This action manipulated a response from Louis, the outcome of which benefitted Cindy, who is therefore likely to repeat the gesture in the future, and the gesture is maintained, over evolutionary time, in this primate gestural repertoire. Notably, the ritualization of gestures here is from a phylogenetical perspective, not an individual one, and thus does not ascribe an individual representation or any cognitive process underlying the behaviour to either party.

This model of communication offers an ultimate explanation of communication with broad taxonomic applicability; the same principles of manipulation and evolutionary fitness that explain the phylogenetic preservation of primate gestures explain the mating display of a bower bird or the aposematism of a toxic insect. This model does not, however, offer proximate explanations for the behavioural patterns of communication; it allows for situations where the induced response of the recipient is the result of *understanding* the manipulation and situations where the induced response is merely *a reaction to* the manipulation, the latter of which requires no cognitive engagement with, or even awareness of, the signaller's desired outcome. There is an opportunity, therefore, for proximate models of communication to elaborate on the means-ends process of communication-as-manipulation by positing the mechanisms that might underlie the communicative behaviours.

2.2. Information Model

Following (Takada, 1954), Marler (1961) proposed the theory of animal communication as information. This model characterizes information as the reduction of uncertainty on the part of the recipient, where the signaller encodes signals with informational meaning, and the recipient can decode these signals to access information. Although the informative signals are not necessarily under the intentional control of the signaller, they are still adaptive, just as in the manipulation model in the sense that they facilitate the desired outcome from the recipient. As a complement to the manipulation model, which more readily explains the fitness benefit of the signaller, the information model explains the adaptive benefit to the recipient more clearly – the recipient can achieve greater fitness by properly decoding the signal, gaining easier access to cooperative, affiliative exchanges, as well as easier interpretation of fearful, aggressive, or competitive displays.

Although the information model, which predates the manipulation model (see Dawkins & Krebs, 1978; Krebs & Dawkins, 1984), is still mainly centred on an ultimate perspective on communication, its principles eventually facilitated research on the cognitive mechanisms underlying communication. The process of giving and receiving informative signals can involve cognitive skills, including semantic encoding/decoding and functional reference (see Table 3.1). Furthermore, within this informational model, signals cannot necessarily be

mapped 1-1 onto meanings, but may demand the use of contextual cues for accurate decoding (Smith, 1977).

Following our earlier example of an exchange between primates, the informational model of communication would interpret the actions via the route of informational transmission. Cindy wants to be groomed, and she encodes this information in a signal – a big, loud scratch across her own chest (Hobaiter & Byrne, 2014). As the scratching behaviour is a non-instrumental signal, meaning that it does not act directly on the body of the recipient, Louis must decode this signal based on contextual cues and existing knowledge of the signal, and in doing so, receives the information that Cindy wants to be groomed. Louis may produce the desired behaviour, or not, depending on the context and the fitness benefit to himself. Not only does this informational perspective address the success of the exchange from the perspective of both the signaller and the recipient, it also opens the door for an element of cognition: encoding and decoding of non-instrumental signals. Although not all informative signals require encoding and decoding – it is equally possible to inadvertently signal information and induce an innate reaction to that information – encoding and decoding become possible under this model of communication, which permits questions relating to cognitive engagement with the act of communication.

The informational perspective, though more robust in its mechanistic considerations, is more a behavioural model of communication than a cognitive one, and thus has theoretical limitations in its ability to fully characterize the cognitive abilities of certain species within communication. It describes cognitive engagement on the level of signal decoding and introduces the concept of flexible interpretation (i.e., varied interpretation of the same signal based on context). It does not, however, address the question of referentiality, at least, not in its earlier iterations (Seyfarth et al., 1980). Vocalizations or gestures encoded with information could be produced voluntarily or involuntarily, while still consisting of a non-instrumental signal encoded with valuable information for the recipient. Modern work within this paradigm (e.g., Tomasello & Zuberbühler, 2002; Leavens et al., 2004), asks this question of intentionality and referentiality, but does not conclusively conclude that the signaller or the recipient have an internal representation of the information, and rather, could be exhibiting "functional referentiality," characterized by signals provoked directly by the external stimuli about which they contain information (Slocombe & Zuberbühler, 2005). Without an ability to account for internal representation of intention and meaning, the informational model of communication is inherently limited to basic, practicable cognitive mechanisms – encoding and decoding – which do not encompass the rich breadth of possible mentalizing in primate communication.

3. Intentional Communication

Intentional communication, also known as goal-directed communication, the third and final historical model of communication, can be considered the first of three fully cognitive models (see Table 3.2). It introduced two critical cognitive skills – intentionality and goal-directed signals. Plooij and Lock (1978) and Woodruff and Premack (1979) were among the first to thoroughly address the question of intentionality in animal communication, specifically in the communication system of primates. They characterized intentional communication as transmission of information between a signaller and a recipient adhering to three main criteria: first, the signaller must be aware the transmission of information will result from the signal; second, the signaller expects that the recipient will similarly be aware of the transmission of information; and finally, the signaller must be able to selectively control their

own signals in order to transmit the desired information. Later work (e.g., Byrne et al., 2017; Hopkins et al., 2007; Tomasello et al., 1985, 1989) on intentional communication follows several core criteria for intentionality, first defined by Bretherton and Bates (1979) for use in developmental psychology. These core hallmarks of intentionality include attentional monitoring, gaze-alternation, persistence, and elaboration.

While at least a subset of these criteria are necessary to indicate intentionality, they alone are not sufficient to conclusively demonstrate it. Townsend et al. (2017) note that, although there is no specific combination of criteria that would absolutely indicate intentionality, more indicators for any particular species or experiment serve as stronger evidence that the intentionality is genuine. Furthermore, we argue that intentionality is most likely to be at work when it is robust in the face of experimental perturbation. If flexible, apparently intentional communication cannot be transferred to a new situation where the old conditions of the successful communicative exchanges do not apply, and exchanges are unsuccessful in this new setting, then the communicative system may be more rigid than initially indicated by successful demonstration of the above criteria. Vail et al. (2013) demonstrated several attributes of intentional communication in coral reef fish (*Plectropomus pessuliferus marisrubri*), theoretically suggesting that intentionality may be more widespread than the complexity of the behaviour might suggest. It is unknown, however, whether the apparently referential signals in fish would stand up under multiple, varied circumstances, which would be stronger evidence of flexible, goal-directed, intentional communication. If it was indeed the case that coral reef fish could successfully transfer this behaviour to a new situation, then there would be no reason to deny the potential for intentional communication in their species. Each of the criteria for intentionality, including flexible transference of the intentionality to new circumstances, has been demonstrated, experimentally or observationally, in primates, particularly great apes (Leavens et al., 2005 for review; Graham et al., 2020).

Table 3.2 Psychological models of animal communication including the signal origins, the signaller's intention, the recipient's decoding, and the cumulative requisite cognitive skills (later models include those of previous ones). A key aspect of inferential communication is that the signaller creates a new signal (or modifies an existing one) to instruct the recipient what to do. X(=x_1+x_2+x_3) is meant to indicate that the signaller provides not just information about their goal, but also instruction about how to do a particular action. Bold lettering in the signaller and recipient column indicates the new component in each model compared to the previous one.

Model	Signal Origin	Signaller's Intention	Recipient's Inference	Cognitive Skills
Intentional Communication	Phylogenetic ritualization Ontogenetic ritualization	I want her to do X for me	n/a (I will do X to her)	Goal-directed signals Intentionality Referentiality Awareness of informational transmission
Inferential Communication	Inference	I want her to do X(=x_1+x_2+x_3) for me	**What does** she want me to do to her**?**	Prosociality Informative intention
Ostensive Communication	Conventionalization Imitative learning	I want **to tell** her to do X for me	What does she want **to tell** me to do to her?	Communicative intention Recursive mental states/ 3rd- and 4th-order theory of mind

Carrying our primate grooming example forward, we now apply the intentional model of communication to these actions. Cindy, the signaller, must first open an attentional channel with Louis, the recipient, ensuring that she has his attention either through the use of an auditory or tactile "attention-getter" signal (Leavens et al., 2005), or by checking for existing visual contact. Cindy must have an internal representation of what she wants – grooming – and an awareness that she needs to transmit information about her goal – her desire for grooming – to Louis. She produces the signal, the big loud scratch from earlier, intentionally, and monitors Louis' response, to determine whether the communication was sufficient to meet her internally represented goal. Louis, the recipient, must attend to Cindy, and must be aware that information is encoded in the signal, thus prompting him to decode it. As before, Louis can provide the desired grooming behaviour, or not, at which point Cindy may persist and produce the gesture again, or she may elaborate, by producing a different signal which can also be decoded to request grooming (see Figure 3.1).

Cindy, in this example, is displaying new cognitive skills compared to those demanded by the previous models of communication. She is engaging in goal-directed communication, where she is internally motivated by her own goal and is using communication as a means of achieving it. She is displaying intentionality, wherein her actions are under her voluntary control, and, at this stage, she is communicating referentially, in that she is making direct, intentional reference to what she wants. Notably, the same cognitive mechanisms are not necessarily required of Louis, other than conscious awareness of the transmission of information. Although, according to this model of communication, he must be aware that there is information to decode, his response to that information does not necessarily need to be voluntary, for the communication to be successful. As in above examples, his response to the information he has decoded could be innate, or externally motivated by the stimulus of the information, rather than motivated by his own internal representation of Cindy's goal.

Figure 3.1 Illustration of two primates engaged in a communicative exchange depicting the recipient's (lack of) inference under the intentional communication model. Illustration by Sadie Tenpas.

Research using the framework of intentional communication has amassed a substantial body of evidence to support flexibility in primate communication (Liebal et al., 2014, for review). Regarding referentiality in primates, several studies have found evidence to support functional referentiality in the vocal domain (e.g., Slocombe & Zuberbühler, 2005; but see Fischer & Price, 2017 for an opposing view), and in the gestural domain (Call & Tomasello, 2020). These are crucial findings for intentional models of communication, and they provide a framework within which to describe some of the flexible and behaviourally complex communication observed in primates from a cognitive standpoint. In our view, however, they still fall short of fully explaining the mechanisms at play in production and interpretation of communicative behaviour in species with complex cognitive engagement during communicative acts. Intentional communication, as a model, invokes a means-ends dissociation, in that it describes observed behaviours in the context of their relevant psychological effects, but does not delve into the actual cognitive processes that permit these cognitive outcomes. It is clear that intentionality and flexibility place cognitive demands on both the signaller and the recipient, but the exact psychological processes are not illuminated. In fact, when we thought that the field was ripe to explore the psychological processes in greater detail, researchers have hesitated to take what we see as the next necessary step in

unravelling the complexity of primate communication. In order to further advance our understanding of the cognitive mechanisms underpinning communication, we need to look beyond intentionality and toward psychological states. We propose the model of inferential communication as a means of explaining and investigating the cognitive, mentalistic aspects of communication, and to form a bridge between existing models of primate communication and the ostensive, language-oriented models found in the human developmental literature.

4. The Model of Inferential Communication

As a theoretical model, inferential communication can be viewed as a system of conveying messages which operates outside the confines of codified, semantic gestures or vocalizations (Wilson, 1998), and which requires the integration of known information and context to interpret informational meaning. While we do not assert that inferential communication is engaged during all communicative interactions in any species, including humans, we submit this model as an explanatory and heuristic tool to investigate communicative behaviour where inferential leaps of understanding, for both signallers and recipients, are required for successful transmission of information. When alternative explanations of apparently successful communicative behaviour are ruled out, it allows for the investigation of higher-order cognitive mechanisms, such as mental state interpretation, prosociality, and, most crucially, *rational inference*. Crucially, in our model, inferential thinking is required of both the signaller, who must account for the leaps of understanding the recipient may make when deciding on the level of ambiguity in the signal, and the recipient, who must infer the meaning of the information being conveyed.

Many authors have noted there is ample evidence that recipients infer meaning from signals (Fischer, 2011; Fischer & Price, 2017; Fitch, 2015; Seyfarth & Cheney, 2017). However, the kind of inferred meaning that we endeavour to investigate differs from other proposals in terms of the type of inference that supports the communication and the type of pragmatics involved. First, we use inference more narrowly than other authors, to distinguish it from other processes. In a broad sense, when a baboon hears the call of his consort behind some bushes, he may infer that she is located behind those bushes (Fischer, 2011). But it is also possible that the individual has learned over time that when that call is produced, a particular female will appear behind those bushes – so an association rather than an inference might be doing the work of deciphering the signal. Another interpretation of "inference" refers the integration of information from multiple sources to make a decision (Fischer & Price, 2017; Fitch, 2015). There is no doubt that integration – putting together disparate pieces of information - is a fundamental aspect of inference (Tolman, 1932; Premack & Premack, 1994). But integration can also be achieved by processes such as conditional discrimination. When a baboon hears a specific female's call, but he also sees that her juvenile offspring are nearby, he may respond differently to her call than if they were absent, not because he has inferred different meaning from her signal, but because he has learned over repeated exposure to similar situations that the appropriate response differs from a situation in which he is alone with the female. In this case, he is not exhibiting inference, but merely learned different responses to different contexts. We agree that inference requires the integration and assimilation of multiple pieces of information to guess at outcomes (i.e. "contextual pragmatics" in Fischer & Price, 2017). But additionally, inference requires that this integration occur in a novel situation, not one that has been encountered before (see Section 6 for an example of how to study this form of inference). Furthermore, our definition of inference affords inferential thinking to the signaller, which allows a greater depth of cognitive engagement, including intended meaning from the signaller.

Second, there is no question that contextual pragmatics play a crucial role in the inferences recipients make in communicative exchanges. For instance, baboons may use the time of the day, the location, the activity or even the reproductive state of their groupmates to derive meaning from signals (Fischer, 2011; Fischer & Price, 2017). In our model of inferential communication, however, we open the door to mental state attribution and even the notion of common ground. We do not ascribe the most elaborate forms of mental state attribution and common ground to the inferences made in our model but propose that more basic levels of mental state attribution, such as knowledge state and past shared experiences, may be taken into account by both parties. This constitutes at least an entry point into a dimension that escapes contextual pragmatics, thus potentially bringing communicative exchanges closer to linguistic pragmatics. Note that our goal is not to downplay the importance of context in deriving meaning. On the contrary, contextual pragmatics play a fundamental role in the communicative exchanges of humans and primates (and possibly other animals), but we argue that there might be more to inference within animal communication than just contextual pragmatics, at least in certain interactions.

We also differentiate our model of inferential communication from the models of ostensive communication (Scott-Phillips, 2015; Moore, 2017; Heintz & Scott-Phillips, 2022), particularly with respect to the nature of inference and the depth of mental state attribution. Models of ostensive communication highlight the importance of inference in communicative exchanges, but they use inference in a much broader sense than we do in our model. Ostensive models also emphasize the role of complex mental state attribution, often articulated as informative and communicative intentions. We discuss and contrast these models with our own proposal in greater detail in Section 5. For now, suffice to say that we conceive inferential communication as the vital missing link between models of intentional and ostensive communication.

One of the main virtues of intentional communication is that it places flexibility and individual use of signals centre-stage. However, the flexibility afforded by this model is rather limited. The origin of signals in intentional communication is either phylogenetic or ontogenetic ritualization. Phylogenetic ritualization produces species-specific signals potentially shared by all members of a species (and other closely related species). Signals *per se* are rather fixed, although their usage can show some flexibility, particularly in the gestural domain, in terms of when individuals choose to produce them, and whether they repeat them or replace with other signals in their repertoire when they fail (Liebal et al., 2014; Tomasello & Call, 2019 for review). This certainly shows some voluntary control over signals, but phylogenetic ritualization cannot produce new signals within an individual's lifetime. This is mainly the task of ontogenetic ritualization whereby two individual shape each other's behaviour over repeated interactions so that they transform instrumental into communicative actions (Pika, Liebal, Call, et al., 2005).

The production of novel signals is an important achievement, but ontogenetic ritualization is a slow process likely governed by associative learning. This means that new signals invariably require repeated interactions before they become fully functional. Attempts to document other forms of learning, most notably imitative learning, have failed to produce convincing evidence this form of learning is responsible for gesture acquisition in chimpanzees (Tomasello et al., 1997; Tennie et al., 2012;). Inferential processes offer an alternative to ontogenetic ritualization and associative learning so that individuals can spontaneously invent gestures that others might be able to comprehend. Inference has been documented in numerous studies of physical cognition in primates (e.g. Hill et al., 2011; Petit

et al., 2015; Völter & Call, 2017). Whether primates can also use inference in communicative situations is unclear but worth investigating. Table 3.3 presents the types of inference that could be involved in primate communication. Each of these types requires increasing levels of cognitive sophistication. In the subsequent sections, we develop our proposal for inferential communication starting with situations involving social inferences in the absence of communication.

Table 3.3 Social inference (non-communicative) and three types of inferential communication presented in ascending order of complexity in terms of the signal production and comprehension. Also depicted is the signaller's intention and recipient's understanding of those signals in reference to the intention communicated by the signaller.

	Concept	Signaller's Intention	Recipient's Inference	Cognitive Skills
Social inference	Instrumental Action	I want to do X	What does she want to do?	Goal attribution
Inferential Communication	Ambiguous Signal	I want **her** to do X $(=x_1+x_2+x_3)$ **for me**	What does she want **me** to do?	Prosociality Informative Intention
	Re-purposed Signal			Innovation Context rationalization
	New Signal			Iconicity Pantomime

4.1. Social Inference

Of all the cognitive skills included in the model of inferential communication, the capacity for inference is both the most obvious and the most critical. Inferential communication is a system which demands a certain flexibility in interpretation of social interactions, where individuals must make leaps of understanding regarding the social behaviour of another actor. One might call this "social inference," defined here as a situational understanding of another's actions beyond the available semantic information. Not restricted to communication, this ability includes successful interpretation of another's goals, intentions, or desires, in both cooperative and competitive contexts. Although social inference is not necessarily within the realm of communication, it is a vital prerequisite to inferential interpretation of another's communicative behaviour. Social inference asks, "What does she want to do?" an open-ended question that relies on behaviour, context, and inference in order to successfully attribute the ultimate goal to a set of actions performed by another.

Take, for example, our grooming primates. Now, rather than describing a communicative exchange, we can use their behaviour to illustrate social inference. In this situation, Cindy grooms herself, producing species-typical grooming behaviours, such as plucking and licking certain areas of the body. She does not specifically intend to produce any particular signal, but she is observed by Louis, who makes inferences about her goals. Louis, observing her plucking behaviour, could mentally represent her goal, which might be to alleviate an itch,

clean a wound, or even to self-soothe after a tense encounter. Louis' inferential interpretation could be based on contextual cues (e.g., a visible wound, having witnessed a fight between Cindy and another individual, etc), and/or past experience (Louis has groomed himself in the past and is aware of the benefits). Louis' capacity for inference, demonstrated here in his differential interpretation of Cindy's actions based on context, invokes the cognitive skill of goal attribution, which is not a requirement for the recipient in any of the previous models of communication. Additionally, Louis shows evidence of addressee awareness, in the sense that he is aware that he is not being addressed, which invites a different interpretation of Cindy's goal than if the behaviour had been communicative and directed at him.

There is ample evidence for social inference in primates, including rational imitation, where great apes were less likely than human children to perform extraneous actions to complete a task, even when those actions had been demonstrated by a human actor (Buttelmann et al., 2007, 2008; Call & Tomasello, 1998). The apes appeared to infer the ultimate goal of the experimenter's actions and were able to produce a different, streamlined set of actions toward the same goal, rather than copying the experimenter's exact movements, indicating that they were able to use the experimenter's behaviour to form a representation of their intentions. While perhaps reflecting less of an inclination toward social learning than human children, who readily imitated both the necessary and extraneous actions of the experimenter, these studies demonstrated that apes were able to infer the ultimate goal of the human's task, and thus eliminate unnecessary steps, suggesting a successful leap in understanding regarding the human's ultimate intention. Great apes also flexibly interpreted an experimenter's behaviour in differing contexts, although the experimenter's actions were identical in both situations. Subjects were more likely to select one of two boxes when the experimenter "intentionally" dropped a marker on it versus when they "accidentally" dropped a marker on it (Call & Tomasello, 1998), which required inferences about the experimenter's goal when dropping the marker. Similarly, apes differentially adjusted their waiting behaviour when experimenters were performing necessary actions on a puzzle box to retrieve food, compared with contexts where those same actions were superfluous, suggesting that they made inferences about the goal of those actions based on different contexts (Buttelmann et al., 2012). In each of these examples, despite identical semantic information, apes flexibly adjusted their responses (e.g., selection behaviours, waiting behaviours, begging behaviours) in response to different perceived goals from the experimenter. This evidence suggests that great apes have the ability to make pragmatic inferences about social behaviour based on clues from context alone.

Evidence of social inference in primates is not limited to the interpretation side of social interactions. When it comes to production, both apes and monkeys show flexible adjustment of vocal signals based on the identity of the recipient (Cheney & Seyfarth, 2018). For example, chimpanzees produce food grunts toward "friends" more often than "non friends" (Schel et al., 2013), and female baboons have been shown to selectively produce conciliatory grunts, mediated by the likelihood that the recipient will view their behaviour as affiliative, where immediate past experience and long-term dominance dynamics appear to be the moderating factor (Cheney & Seyfarth, 2012). Audience effects such as these have been noted as evidence in reviews of intentional communication in primates (Liebal et al., 2006; Byrne et al., 2017), but they also present a potential case for inferential cognition, if and when these signals are voluntarily produced or withheld. While changes to vocal signals according to varying situational context (Seyfarth & Cheney, 2010 for review) are not enough to suggest social inference, variation in communication behaviour regulated by *social* context, combined with voluntary control of these signals, allows that signallers may have an

awareness that the intended message may be received differently by different individuals, depending on the existing social relationship with the specific partner. The possibility that primates can flexibly adjust communication behaviour based on the varying potential outcomes from different recipients suggests that they have may be able to base these decisions on inferences from past social experiences, which goes beyond the realm of mere intentionality.

4.2. Inferences Using Communicative Signals

4.2.1. Ambiguous Signals

In the case of fixed, semantic, unambiguous signals, advanced cognitive mechanisms are not necessarily required. In the case of flexible, ambiguous signals – those which are used in multiple contexts to mean different things – inference is a necessary component of interpretation. In order to apply social inference to the realm of communication, we must first consider the mentalized question at hand, for both the signaller and the recipient. The signaller asks, *"What do I want **him** to do?"* This question involves both an informative intention (that which she wants him to do), and a prosocial desire (the fact that she wants or needs him to do it, at no immediate benefit to himself). The recipient, on the other hand, asks, *"What does she want **me** to do?"* This question has an inherently prosocial component, which denotes a new cognitive skill, not explicitly required by past models, on the part of the recipient.

This arrangement requires the signaller to transmit a message which relies on the recipient's capacity for inference in order to be fully interpreted. She must establish attentional contact with the recipient to open a channel of communication between them, and must request help, providing instructions as to the nature of the help required. If she uses an ambiguous signal to provide instructions, however, the recipient must use inference to successfully interpret the message. For example, returning to Cindy and Louis, we now imagine a situation in which Cindy wishes to be groomed by Louis. She faces Louis, ensuring that he observes her, which opens the channel of communication. She taps her knuckles against the ground and bobs her body up and down, a gesture which is commonly used to initiate play, but has also been observed preceding grooming (Tomasello et al., 1997). In this gesture, she has both requested help from Louis, and provided instructions – she wants help in the form of grooming. She has, however, relied on her knowledge of the contextual inferences Louis is most likely to make, as well as the belief that Louis will be sufficiently motivated to help her. Louis, for his part, must attend to Cindy, be motivated to help, and understand the instructions, using context to disambiguate her gesture. If the communication is successful, then Louis will use contextual cues (for example, past experience with Cindy, in which they have rarely engaged in play) to interpret her instructions, and he will infer that she wants to be groomed (see

Figure 3.2).
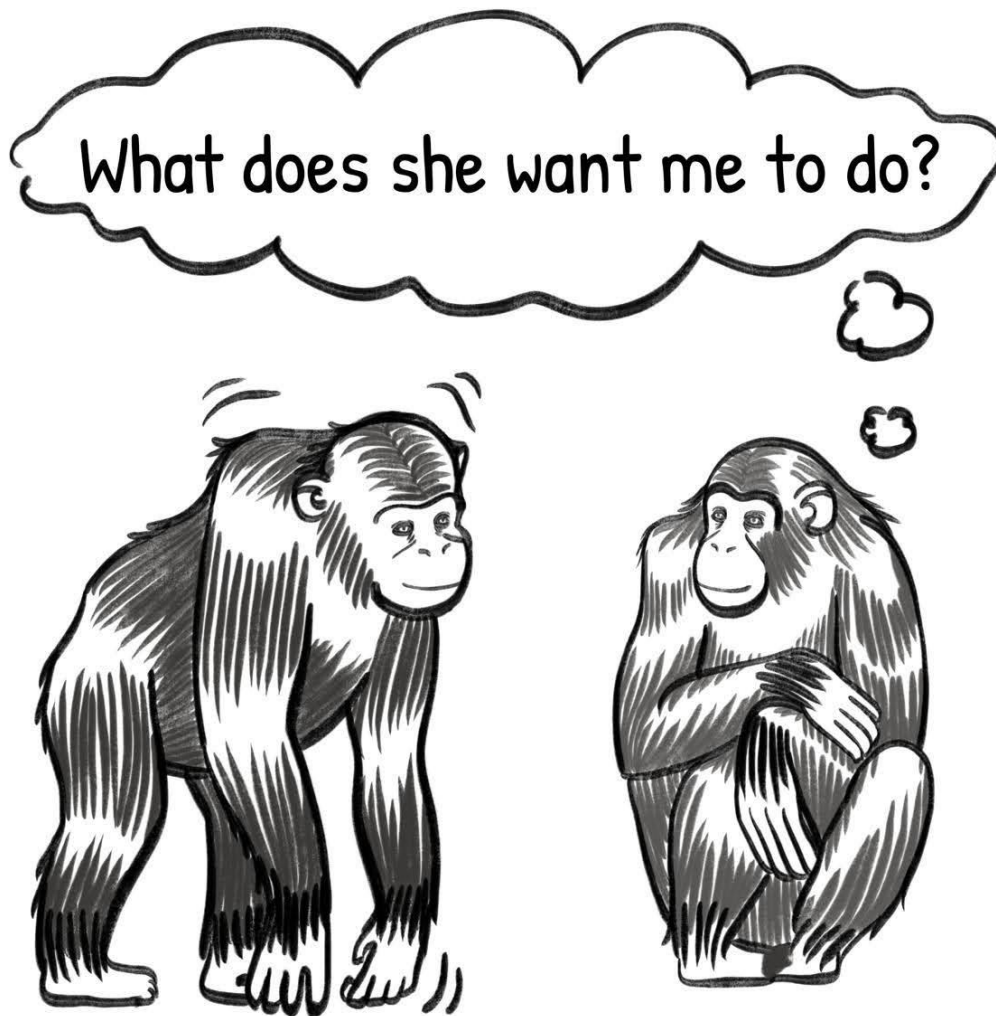
Figure 3.2 Illustration of two primates engaged in a communicative exchange using ambiguous signals, depicting the recipient's inference under the inferential communication model. Illustration by Sadie Tenpas.

Regarding flexible interpretation of ambiguous behaviour, there is evidence that primates are capable of such inferences. For example, great apes successfully differentiated between the same action from a human experimenter, producing more begging and impatience behaviours when the experimenter's action could be interpreted as "unwilling" to provide food versus "unable" to provide food (Call et al., 2004). From the production side, apes were able to modify the shape and location of their pointing behaviour when their options were arranged such that a simple forward point would be ambiguous, suggesting that they recognized the need to disambiguate their pointing for the experimenter's successful comprehension and that they were able to apply that understanding to their actual gestures (Tauzin et al., 2020). Furthermore, great apes will monitor the success of a relatively ambiguous signal (e.g. begging), and elaborate with different, additional gestures (e.g. pointing at the desired option), if the desired outcome is not achieved (Leavens et al., 2005). This demonstrates a willingness to produce ambiguous signals, suggesting that the apes have some expectation that the signals will be successfully disambiguated by the experimenter, and also the capacity to choose whether or not to be more specific, at potentially higher cognitive cost to the signaller, if the ambiguous signal fails.

4.2.2. Re-purposed Signals

In situations where an ambiguous signal made unambiguous through inferential interpretation is not sufficient to thoroughly instruct the recipient, the signaller may turn to other resources to produce an instructive signal. One possible approach is to use an existing signal within the communicative repertoire, but in a brand-new context, relying on the inferential capability of the recipient to interpret the familiar signal in a new way. The situational question remains the same for both the signaller and the recipient – "What do I want him to do? /What does she want me to do?" – but new cognitive skills are required at this level of complexity. In addition to the required capacity for inference and prosocial behaviour, the signaller and the recipient must both take a creative leap and rationalize the otherwise nonsensical use of the signal in the current situation, giving it new meaning.

If we follow primates Cindy and Louis into a new situation, an experimental setting in which they must work together to open a puzzle box, we can hypothesize an interaction using this form of inferential communication. Cindy wants Louis to help her open a locked puzzle box, which can be achieved by turning two wheels, simultaneously, at opposite ends of the box. As neither can reach both wheels, they must coordinate to solve this problem. As before, Cindy must establish a communicative channel with Louis, by looking at him and ensuring that he sees her. As no fixed, semantic gesture exists in their shared repertoire to communicate "help me open this box," Cindy produces a gesture more typically used to beg for food, a mouth stroke (Tomasello et al., 1997). The gesture is nonsensical in this context, as Louis has no food to offer her. Instead, Cindy has engaged in creative use of this gesture to encourage Louis to open the box with her. If this exchange were to be successful, Louis would correctly infer that Cindy does not want to share food, rather, he would rationalize the otherwise pointless gesture to a new meaning, and if sufficiently motivated, help Cindy open the box (see Figure 3.3).
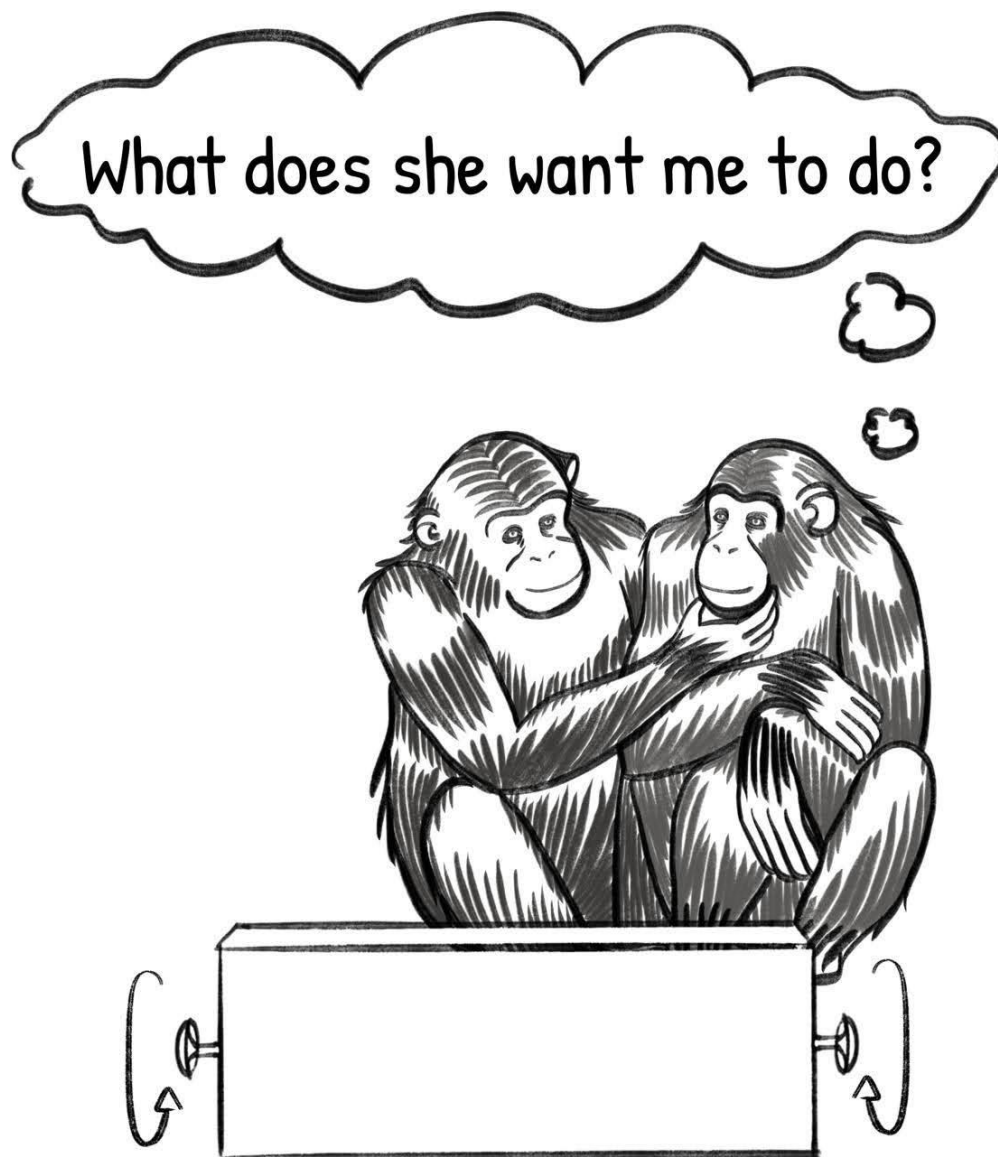
Figure 3.3 Illustration of two primates engaged in a communicative exchange using re-purposed signals, depicting the recipient's inference under the inferential communication model. Illustration by Sadie Tenpas.

This exchange relies on creative re-purposing of existing gestures, a capacity which has not been conclusively demonstrated in primates, but which can be hypothetically proposed in the model of inferential communication. Armed with this framework, it is possible to design experiments which more specifically demand this ability, to explore the cognitive skill and its presence or absence in primates.

4.2.3. New Signals

In its final possible level of cognitive complexity, inferential communication provides a platform for two actors to create an entirely new signal, rationalized and understood by both purely based on the context and their own capacity for inference. Still adhering to the question, "What do I want him to do?", the signaller instructs the recipient using an iconic gesture – one that does not exist in the known repertoire of the individual, and which

pantomimes the action she is requesting that the recipient perform. This iteration of inferential communication adds two specific cognitive skills not required for earlier levels: iconicity and pantomime, which are necessary for both the signaller and recipient.

If we return to Cindy, Louis, and the puzzle box, we can imagine a situation in which Cindy establishes that she has Louis' attention, and then turns her hand in the air, miming the turning of the wheels on the puzzle box. Louis, observing this pantomime, interprets the gesture as an iconic representation of the desired action, understands Cindy's request for help and the instructions she has given, and helps her open the box (see Figure 3.4).
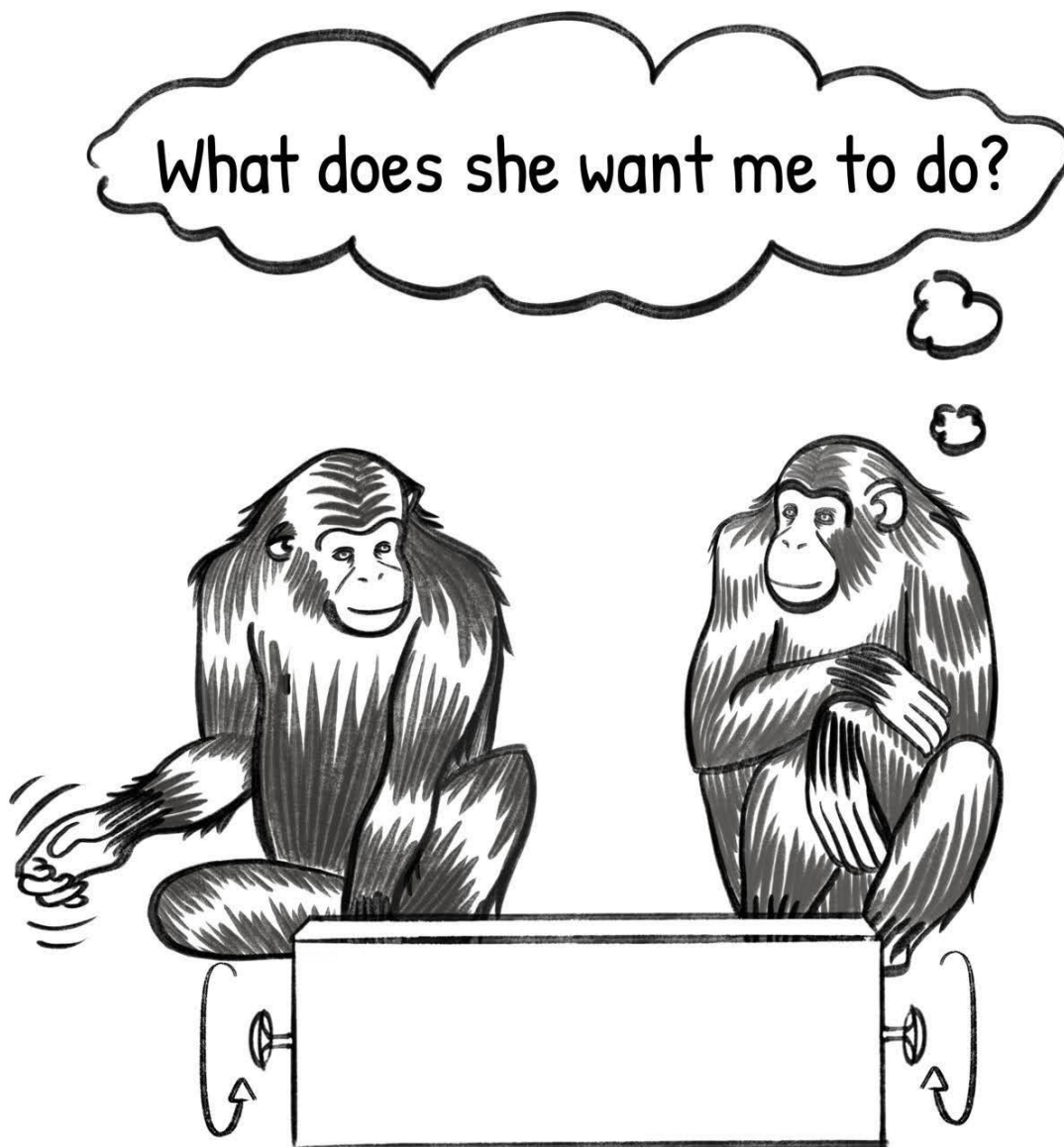
Figure 3.4 Illustration of two primates engaged in a communicative exchange using pantomimed signals, depicting the recipient's inference under the inferential communication model. Illustration by Sadie Tenpas.

While this type of interaction has not been systematically documented in primates, and it is unlikely that this type of interaction is common, preferred, or cognitively efficient for non-human animals, the question remains as to whether primates could exhibit these cognitive abilities if there were no other way to solve the problem. There is some anecdotal evidence that primates are capable of the two new cognitive skills seen here – iconicity and

pantomime. Grosse et al. (2015) found that one chimpanzee, who had been partially reared by humans, engaged in an iconic gesture when a human experimenter required instruction to operate an apparatus. Additionally, great apes have been anecdotally observed engaging in pretend play, with or without the assistance of objects, suggesting some possibility of iconic representation of objects (Gómez, 2005). On the comprehension side of these abilities, great apes have been shown to learn locations associated with iconic gestures faster than locations associated with arbitrary gestures, suggesting that they have some ability to link the iconic nature of those gestures to their representational meaning (Bohn et al., 2016a). It is noteworthy that production of iconic signals, iconic play, and imitation of pantomimed gestures can be scaffolded with the support of physical objects, removing the requirement of intransitivity that is intrinsic to true pantomime (e.g., Call, 2001; Gómez, 2005; Tennie et al., 2012). This suggests that iconicity and pantomime are challenging cognitive skills for great apes and would require substantial prosocial motivation or necessity in order to be a cognitively efficient mechanism. Whether these anecdotal cases could be transformed into robust evidence of these cognitive skills in primates, especially in the absence of scaffolding, is unknown, but the question itself presents an exciting example of the investigations and experiments that become possible on the tails of inferential communication. It also invites the question of prosociality in primates, given that prosocial action is a critical component of the success of any inferential communication exchange, but especially those with increasingly difficult cognitive demands.

4.3. Prosocial Motivation

One of the basic tenets of human communication is that it is a prosocial and cooperative enterprise (Hare, 2017). Although prosocial motivation can foster communicative exchanges, and it may be needed for language acquisition, we argue that it is not necessary for inferential communication because effective exchanges can occur even in the absence truly prosocial (i.e., altruistic) behaviour. Apparently prosocial actions, required of both actors in inferential communication exchanges, can be understood with several different motivations in mind. On the surface, prosociality is defined as any action, whether requested or performed, that one actor completes for the benefit of another, with either no benefit or actual cost to themselves (Cronin, 2012). In practice, however, apparently prosocial actions, those performed at cost of one individual and benefit of another, may have motivations other than pure altruism. An individual could be motivated to behave in a prosocial manner due to a cost-benefit analysis, in which the continuing annoyance or harassment from the requesting individual is a greater cost than performing the action, and the actor is therefore sufficiently prosocially, if not altruistically, motivated. Alternatively, the actor could incur hidden ultimate benefits, such as augmented reputation, hopes for reciprocation, or, in humans, a proximate benefit of internal moral good feeling, which offset the apparent cost of the prosocial action. Thus, when we argue that prosociality is a requirement for successful inferential communication, we refer to the broad spectrum of motivations that could lead to apparently prosocial action. Apparently prosocial actions, whether altruistic or otherwise, have been observed in several species of primate, from tamarins (Cronin et al., 2010) to macaques (Massen et al., 2010), to great apes (Pelé et al., 2009).

Altruistic prosocial motivation and willingness to engage in the inherently cooperative act of communication become more imperative as the cognitive load of the exchange increases. For the both the signaller and the recipient in a communicative exchange, the cost-benefit analysis of the effort to produce or interpret a communicative signal changes depending on the difficulty associated with interpreting the message. For fixed signals and ambiguous but

commonly used signals, the cognitive effort may not override the beneficial outcome of the signaller and the potential hidden benefits for the recipient. When the more demanding cognitive skills mentioned above – creativity, rationalizing re-purposed signals, iconicity, and pantomime – are necessary for the exchange, the outcome must be more beneficial for both parties. Particularly for the recipient, it may be that this type of cognitive load is only worth the effort if the individual is truly altruistically motivated, a phenomenon which remains debated in primates (Cronin, 2012). Perhaps prosocial motivation is crucial to decode opaque messages that otherwise are simply not understood and consequently, ignored. It is possible, therefore, that lack of existing evidence for these later levels of inferential communication is caused by twofold limitations. First, the necessity for truly altruistic motivations, which appear to occur sparsely, if at all, in primates, and second, the difficulty of the cognitive mechanisms at play. It is possible, however, that in the presence of sufficient prosocial motivation, primates could produce and interpret these types of cognitively complex signals.

5. Beyond Inferential Communication: Ostensive Communication

Although our focus is on inferential communication, it is critical to discuss ostensive communication for the sake of contrast and completion. Ostensive communication makes the leap from social inferences to communicative inferences – specifically, inferences about communicative intention (see Table 3.2). Communicative intention is traditionally understood as a mental state function, in which the communicator not only knows the mental state of the recipient, but consciously intends to manipulate that mental state by making their own informative intention manifest. This is combined with the recipient's recognition that the communicator has an informative intention, which prompts the recipient via the presumption of relevance to make inferences about the meaning of the message based on contextual cues and mental states (Scott-Phillips, 2015). The capacity of primates to produce and comprehend communicative intention under this mentalistic definition is not clearly understood – it has yet to be conclusively observed or experimentally demonstrated in great apes, and it is seldom investigated in monkeys and prosimians (Moore, 2016). Some researchers assert that this cognitive capacity is unlikely to exist in primates, given the sufficiency of a sparser, more goal-directed and intentional model of communication to explain most communicative exchanges primates (Fischer & Price, 2017), and given that primates frequently fail tasks which require production or comprehension of communicative intention (Tomasello, 2008). This mentalistic definition of communicative intention requires recursive mental state attribution, including fourth-order theory of mind (Scott-Phillips, 2014), which many regard as too complex for primates.

Ostensive communication asks the question, *"What does she want **to tell me** to do?"* where not only the informative intention, but also the communicative intention, is manifest to the recipient. In our hypothetical primate example, Cindy wishes to be groomed by Louis. In order to accomplish this, Cindy makes inferences about Louis' current mental state – his willingness to groom her, his awareness that she wants to be groomed, and their existing shared knowledge – and knowingly and intentionally sets out to alter his mental state with her message, such that he becomes aware that she wants to be groomed and is motivated to do so. Louis, likewise, as the recipient, must be aware that Cindy is attempting to alter his mental state, and uses that knowledge to make inferences about what she wants, based on the situation context.

Our model of inferential communication shares two key aspects with the model of ostensive communication: inference and mental state attribution. However, it differs in the type of

inferences that it uses, and it lacks the most complex forms of mental attribution, particularly communicative intentions. Models of ostensive communication use inference with two meanings, one very broad (all communication involves some form of inference) and one rather narrow. For instance, (Scott-Phillips, 2015) describes inference as the interpretation of meaning based on evidence of informative and communicative intentions of the signaller. In our model of inferential communication, we do not ascribe expression or interpretation of communicative intention to either actor, but rather suggest that the signaller is relying on the recipient to make inferences about their goals (i.e., informative intention), rather than their communicative act itself. Thus, although we agree with Scott-Phillips (2015) and Heintz and Scott-Phillips (2022) that communicative intentions may be beyond the capabilities of non-human animals, we argue that informative intentions might not be – signallers can express their goals informatively, but do not make their intentions manifest and recipients do not necessarily use presumption of relevance to infer meaning.

Recently, Heintz & Scott-Phillips (2022) distinguished between 'intentional expression' defined as the expression of mental states (e.g., a signaller may indicate what she wants to a recipient) and ostensive communication that requires making informative intentions manifest. We view intentional expression as similar (if not equivalent) to what we are calling inferential communication, except that we argue that informative intentions (perhaps in a more rudimentary form) are conveyed by signallers, but communicative intentions are not. Other authors have argued that nonhuman animals may even exhibit some forms of communicative intention. Moore (2017) argues that primates may indeed exhibit a form of Gricean, ostensive-inferential communication, but emphasizes the role of awareness of address on the part of the recipient to provide the context for interpretation, which is followed by inferences about the goal of the signaller.

The complexity of mental state attribution required by full-blown (human) ostensive communication is not yet evidenced in primates. Like the more complex levels of inferential communication, it is possible that both the cognitive and the prosocial demands are too great for the majority of communicative exchanges between primates. Perhaps, with evidence taken from an inferential communication framework, it might be possible, in the near future, to design experiments which better establish the limits of primate mental state attribution, to further bridge the gap between language-oriented developmental literature, with rich, Gricean interpretations of communication, and comparative literature, where interpretations are currently limited to description and suggestion of cognitive engagement. The model of inferential communication, when applied to observations and experiments in non-human animal behaviour, presents the opportunity to ask theoretical questions about flexible communicative problem solving, theory of mind, and communicative intention.

6. Practical Applications of Inferential Communication

Any newly proposed theoretical framework to study animal communication, has to consider its practical applications: what can this model offer, how can it be examined empirically, and which species are more likely to display it? In this section, we highlight some of the specific applications of inferential communication and propose some examples of experimental designs to test whether recipients, but also signallers, use inference in their communicative exchanges. To do so, we present three tasks, one using vocal communication and focused on inferred meaning, and the two others using gestures and focused on intended meaning. We intentionally provide methods examining both vocal and gestural communication in order to illustrate the complementary roles played by vocal and gestural communication in elucidating

the intended and inferred meaning of ambiguous, re-purposed and novel signals. We close this section by outlining our criteria for determining whether a species might be a good candidate to investigate inferential communication.

A key application of inferential communication is to explain the origins of some gestures. It is recognized that gestures can arise via phylogenetic or ontogenetic ritualization (Cartmill & Hobaiter, 2019). Another mainly discarded form is third-person imitation (Tomasello et al., 1997; Tennie et al., 2009), although language trained apes have been reported to learn some signs by imitation (Fouts, 1972; Gardner & Gardner, 1990). We propose that inference could serve as a fourth form of gesture acquisition; creating a new gesture to indicate old or new meaning, or less demanding, re-purposing a gesture, and here the work is in using it with a different meaning and especially interpreting it. Different from phylogenetic ritualization, where a successful gesture is preserved and inherited in the innate repertoire, and ontogenetic ritualization, where a gesture develops from repeated use of action-oriented movements, inferential development could explain gestures which originate as iconic or re-purposed movements and are practiced and used until they are semantically established between two or more individuals. Notably, this understanding of the origin of gestures would differentiate between ritualized gestures which iconically evoke the requested action, but evolve from the actual occurrence of the action, and inferred gestures, which originate from an iconic, pantomimed representation of the action.

It is crucial that inferential communication, as an origin of gestures and as a cognitive process, be explored experimentally. Novelty is an essential part of the development of new gestures; if two individuals use a gesture repeatedly, there is no need to invoke inference. Inference need not necessarily be applied in all communicative exchanges, but when the system is perturbed (new conditions or old conditions no longer apply) it can play a crucial role in the success of communication. Once invented by inference, a gesture may be used repeatedly, which can quickly mask its origins. Thus, experiments are critical in order to observe the emergence of new forms of communication.

In designing experiments to test inferential communication, it is essential to ensure that the task requires true inference – the integration of known information to understand a new scenario. Likewise, the experiment should require the use of pragmatic information on the part of both parties, not just on the order of situational context clues, but on the mentalized level of knowledge state, private interaction history, or individual preferences. Our first proposed experiment applies these two criteria to interpreting ambiguous vocal signals. We imagine an experimental setting in which the recipient of the communication knows two established pieces of information, which may have been learned by past inference, association, or simply occurred as a result of the individual's maturation. The point is that the origin of the two pieces of information is not so relevant in our example. First, the recipient, a primate in this example, must be familiar with the species-specific vocalizations that individuals produce when they discover a cache of highly preferred food. Second, the recipient must be familiar with the individual food preferences of a particular groupmate. For instance, Cindy, our recipient, knows that Louis likes bananas but does not like grapes. This is something that she could have learned by observing Louis' feeding patterns: always eating bananas with gusto but ignoring grapes, when both are available, and even when bananas are gone, Louis shows no interest in grapes still available. Cindy is also familiar with their species-specific food calls, which are associated not with a particular type of food, but with the discovery, prior to, but not during eating, of a cache of food.

In the test condition, Cindy is shown that one of two foods is hidden behind a bush, but she is not shown which type of food. Louis then appears and produces a food call upon encountering the food cache. If Cindy is indeed capable of integrating multiple pieces of known information to infer meaning in this new situation, we predict that she should infer that there are bananas behind the bush. Moreover, she should be surprised, in this instance, to search and discover grapes behind the bush, and this response pattern should be reversed if the caller was an individual who likes grapes and does not like bananas. Notably, experiments like this allows examination of the first exposure to this novel situation, which is important for evaluating inference. Associative processes require at least one event for learning to occur, which means the recipient's reaction on initial exposure in the proposed experiment is a measure of true inference. As far as we know, this proposed experiment has not been done (but see Shorland et al. (2022) for a similar experimental paradigm), but we already know that chimpanzees integrate the food preferences of others and their visual access when choosing between two experiments – selecting the one which will give them the most favourable outcome (Eckert et al., 2018). This experiment would test whether they could extend this ability to integrate information to inference in communicative exchanges. Compared to the work investigating recipient comprehension, much less has been done examining the inferential abilities of signallers, with some authors arguing that primate signallers do not intend meaning, recipients just infer it (e.g., Fischer, 2013; Fischer & Price, 2017). This is a sensible proposition given that primate vocal signals are fixed, apart from variation in the timing and context of their use. Such inflexibility in vocal production may not permit primate signallers much opportunity to imbue meaning to their signals. Gestures, on the other hand, are quite different in terms of their production. Gestures grounded in bodily action; they are much more flexible than vocalizations, which opens the door for flexible variation that changes the potential interpretation of the signal. This flexibility also permits the creation of novel signals or the re-purposing of old signals to a novel use. Therefore, we challenge the idea that primate signallers in general do not ever intend meaning and argue that this conclusion may have resulted from asking this question from the perspective of vocal communication only.

The literature already contains some studies illustrating this point – examples we would argue indicate that signallers communicate intended meaning. For instance, Bohn et al. (2016b) found that great apes used a pointing gesture in an unusual way (pointing to an empty dish) to request food that was no longer in that dish. Pointing to an empty dish is atypical for apes, especially given that another dish containing food that was less preferred, but otherwise perfectly acceptable (they always ate this food in control trials), was present. Special care was taken to avoid training the apes to point to an empty container in the pre-test, where they witnessed that the experimenter got up as soon as the food was depleted, left the room, and brought in more food, without giving the subject a chance to point to the empty container. Importantly, apes only used this unusual gesture with an experimenter who had brought food in the past as soon as food had been depleted but not with an experimenter who had given them food but not brought it in the first place.

When we analyse the key features of this case, we conclude that pointing to an empty container qualifies as re-purposing a familiar gesture to communicate about an absent referent. First, pointing with extended fingers, unlike vocalizations, is not a species-specific gesture, but one that is acquired in contact with humans, thus showing some degree of flexibility in gestural acquisition. Second, the pointing gesture is directed at referents (e.g., food item) that are present (even when they are hidden), not to empty dishes, which suggests that the apes in the experiment were using the gesture in a novel way. Third, apes used the

pointing to the empty container only with the experimenter that they had experienced bringing food, and not with others, suggesting that they accounted for the private interaction history between themselves and the experimenters in order to inform their knowledge of whether the gesture to the absent entity would be meaningful. There are other examples in which apes communicated what they wanted by re-purposing an action to request help from an experimenter. The bonobo Kanzi pounded on a nut to request that an experimenter to crack it open (Savage-Rumbaugh et al., 1986). In anecdotal observations, juvenile gorillas physically guided human researchers toward locked doors, using gaze-alternation throughout the movements, presumably to indicate to human observers what needed to be done (Gómez, 1990). The fact that in these instances apes established eye contact with the human experimenter when performing their actions toward the door and reduced their rate of these door-approaching actions when the experimenter left the room strongly suggests that the apes were using those acts to communicate with the experimenter, and not purely as a goal-oriented mechanism.

Intended meaning could also theoretically occur in more complex forms of communication, whereby apes invent a new gesture by, for example, pantomiming an action to indicate the tool that they require to obtain food. Yamamoto et al. (2012) reported that chimpanzees transferred tools to their partners following requests. Signallers used a hand begging gesture and recipients, who could see the kind of tasks that signallers were facing, selected the correct tool from an assortment of various tools and gave them to the signaller. When the recipient's view of the signaller's task was blocked, however, they handed tools randomly. This means that the begging gesture itself did not carry meaning about the type of tool. Context provided that information because the recipient could see the tool that was needed. Thus, the burden of decoding the message fell on the recipient who used contextual cues (the type of apparatus present) to infer meaning. This level of inference is based on contextual pragmatics, not mental states, but it begs the question: would the signaller become more specific in her request, and perhaps even invent a novel gesture perhaps pantomiming the use of a specific tool, if the lack of contextual information persisted over time? We think that this might be asking too much from signallers, who seem to have trouble producing intransitive actions in imitation studies (Tennie et al., 2012). Thus, a pounding action to indicate a stone hammer might be outside of the spontaneous repertoire of primates, but if the intransitive action could be scaffolded with transitive elements, it might be possible that primates could gesture with intended meaning using novel signals.

In this potential experimental arrangement, with the possibility of scaffolded novel gestures, it is possible to examine whether signallers would take the context into account when producing their signals, which would suggest an awareness of the inferences they can reasonably expect the recipient to make. If the context already provides enough information about their intended meaning, would their signals become less specific, particularly when more specific signals are costlier to produce? Conversely, if contextual cues are ambiguous, would signals become more specific? There exists some experimental evidence that apes use pointing variations to disambiguate between two food items when the higher-value food was placed behind a lower value food and subjects were asked to select their preferred food, via pointing (Tauzin et al., 2020). A similar paradigm could investigate whether apes use modified pointing gestures to disambiguate between choices where the context is identical, but their knowledge of the recipients' past experiences or preferences is varied. For example, if one experimenter is known to always provide the higher-value food regardless of the spatial arrangement of the plates, but another experimenter is new to the situation and has no

expected pattern of behaviour, will the subject use modified pointing gestures to disambiguate their choice with the new experimenter, but not the familiar one?

We now turn our attention to criteria for determining which taxa and which species might be more likely to display inferential communication. Based on the examples that we have given, primates, and particularly great apes seem suitable candidates to investigate the existence of inferential communication. While the communicative behaviour of many species is sufficiently captured by explanations found in the foundational models of communication, it is possible that other species, apart from primates, may also be capable of inferential communication provided they possess the required cognitive prerequisites. We propose three such prerequisites: goal-directed communication, general inferential reasoning abilities, and non-communicative social inference. If evidence of these abilities is found in any species, regardless of taxa, it is possible that inferential communication may be within their capacity as well. For example, there is a body of evidence that canines exhibit intentional communication (e.g., Rossi & Ades, 2008) and social inference (e.g., Bräuer et al., 2006). African grey parrots have been shown to exhibit general inferential abilities (e.g., Pepperberg et al., 2013, 2019; Schloegl et al., 2012), and there is some evidence to suggest that they possess the capacity for intentional communication as well (e.g., Pepperberg, 2004). These groups may, therefore, be promising candidates for inferential communication, but rigorous testing of the above pre-requisites would be necessary before investigations of inferential communication could be practically conducted in any of these groups. We do not suggest that any species meeting these criteria is de facto likely to use inferential communication, we merely suggest that possession of these prerequisites may serve to determine whether that species is worth closer investigation.

In sum, we have proposed several ways by which inferential communication can be used to investigate inferred meaning by recipients using true inference – the integration of information to be applied to a new scenario – as well as contextual clues based not only on situational factors, but also on the mental state of the signaller. Furthermore, we have highlighted some tasks already present in the literature that we believe test for intended meaning on the part of a signaller, and proposed ways that they could be modified to new tasks to investigate whether primates can integrate simple theory of mind into their accounting of context, and whether signallers can account for such context while producing more complex (in terms of iconicity) forms of communication. We also indicated that a species possessing goal-directed communication, general inferential reasoning abilities, and/or non-communicative social inference (with all three abilities constituting the strongest foundation) would be a good starting point to investigate inferential communication.

7. Concluding Remarks

The field of animal communication has made considerable progress since the appearance of the early ethological models purely based on behaviour. Much of this progress has occurred as a consequence of the development of cognitive models of animal communication. In what has otherwise been a progressive increase in cognitive sophistication aimed at explaining flexible communication, we think that the field now runs a risk of stagnation due to the rejection of any form of mental state attribution in communication (Townsend et al., 2017). In this paper we have argued that we need a more thorough and detailed understanding of mentalizing in communication, particularly for species that are flexible communicators, and especially when those data are subsequently used to make inferences about the evolution of language. Without mentalizing in models of animal communication, the gap between animal and human communication might be too wide to bridge.

We submit the model of inferential communication as a way forward – a way to progress from descriptions of potential cognitive outcomes to considerations of the actual cognitive mechanisms driving them. Evidence of cognitive forms of communication in primates, especially intentional and referential exchanges, combined with evidence of social inference such as goal attribution, leads us to propose that primates (and perhaps other species too) may have the capacity to make inferences within communicative exchanges. The idea of inference playing a role in animal communication is not new, but we argue that its potential importance and scope has not been fully realized because inference has often been conflated with other mechanisms. Moreover, we propose that investigation of inferences involving the integration of disparate pieces of information, some not based on contextual cues, may provide new insights into the mechanisms underlying the complexity and flexibility of primate communication. Our model invites a rich interpretation of the cognitive mechanisms surrounding communication by challenging the idea that meaning is drawn exclusively from a set of rules or semantics, or from conditional discrimination between situations, which might otherwise suggest simplistic associative learning or hardwired signal-response connections. We also decouple informative intention from communicative intention and suggest that it is possible for actors in a communicative exchange to engage with simple mental state attribution and expression of goals, absent the recursive levels of theory of mind found in ostensive models of communication.

The model of inferential communication is a multi-level framework, beginning with social inferences regarding non-communicative behaviour and extending to communicative inferences regarding how signals are used and interpreted, including consideration of the motivation underlying communicative exchanges. With regard to signals, we have illustrated the inferential approach to interpreting ambiguous signals, re-purposing old signals, and creating new ones. Each level shares the fundamental requirement that both individuals, the signaller and the recipient, must make leaps of interpretation for successful communication. For some of these levels, there is already some evidence suggesting that primates might be capable of communicative inferences, but for other levels there is only anecdotal or even negative evidence. Furthermore, we have proposed ways in which these ideas could be tested using new tasks or by modifying existing ones. With regard to motivation, we have argued that a prosocial motivation is not strictly necessary for this form of communication to arise because it can hijack other motivational systems for the same successful outcome, but if present, it may facilitate successful communication involving the production of novel and initially opaque signals.

Our proposal extends beyond current approaches to referential and intentional communication but stops short of ostensive communication. Although we do not rule out *a priori* the possibility that ostensive communication could occur in primates, we suggest that before tackling this issue, is important to explore the possibility of inferential communication, which is in some ways a pre-requisite for ostensive communication. Our proposal therefore does not qualify as mentalistic communication in the Gricean sense (Grice, 1957; 1969; 1989) but unlike Townsend et al. (2017) it does not flatly reject the importance of some forms of mentalizing, which we incorporate to our model. Namely, we argue that goal attribution, visual perspective taking, and knowledge attribution may play an important role in the inferences that individuals make in their communicative exchanges.

Finally, our endorsement of inferential communication should not be taken as an indication that we believe primates engage in inferential communication in every communicative exchange. Instead, we propose that individuals mainly engage inferential communication

when routine conditions change, and new solutions are required. In this sense, engaging inferential communication is analogous to engaging cognitive control and monitoring mechanisms in problem solving following the perturbation of a previously stable system. We believe that inferential communication is ideally placed to bridge the gap between the intentional and the ostensive model of communication, something that it is particularly important for those wishing to make inferences regarding the evolution of language. It is a framework that we hope will contribute to more precise descriptions of phenomena we have already witnessed in primates and promote new insights into the complexity of animal communication. It is a toolkit – a perspective that we hope will empower researchers to take a more productive approach to animal communication, both in design and interpretation.

Chapter 4 Mediating Gaze-Following and Double Looks with Ostensive Behaviour

Abstract

Existing research into the capacity for ostension in non-human primates has been limited by a range of methodological factors, especially experimental designs that are oriented around behaviours such as pointing and declarative sharing of information. In order to investigate the capacity for ostension without these limitations, I looked to alternative measures of production and comprehension of communicative intention. Previous studies of gaze-following in primates have suggested that some species do expect others' gaze to be referential. These studies point to the phenomenon of "double looks," or double checking an empty spatial location at which another agent is gazing, as evidence that an expectation of information has been violated, inducing the subject to look again. The purpose of this investigation was to explore certain primate species' sensitivity to ostensive communication, using double looks as a proxy for expectation of information. In the current study, I measured the effect of ostension on the rate of gaze-following and double upward looks in 71 individuals across seven primate species (orangutans, gorillas, chimpanzees, bonobos, siamangs, buff-cheek gibbons, and brown capuchin monkeys). In the ostension condition, I called the subject's name and bounced my body in an affiliative gesture, prior to orienting my head and eyes upward. This display was compared to an attention-getting but not communicative display, in which I pretended to eat a piece of food, and a control (neutral behaviour) display, to parse the effects of ostension versus mere establishment of attention. The results showed that while subjects were equally likely to produce initial upward looks across conditions, they produced double looks significantly more often in the ostension condition only. These results support the hypothesis that primates' expectation of information from gaze can be increased by ostensive communication, and that this response cannot be explained by increased attention. I interpret this evidence to suggest that certain primates form referential expectations in response to ostensive signals. To expand upon this finding, I propose potential methods to deepen and clarify our understanding of primates' cognitive engagement with ostensive communication.

Introduction

In the majority of the published empirical work explicitly examining the interpretation of ostension in non-human primates, the subjects are on the receiving end of communicative behaviour from a human, often with the intention of transmitting a message about the location of food or another desired object (e.g., Call et al., 2000; Byrnit, 2004; Moore et al., 2015, also see Chapter 2). Most of these designs also measure comprehension using a trained behaviour such as pointing or exchange of objects, which is directly solicited by the experimenter and is a necessary step toward receiving a food reward. These paradigms generally show a lack of evidence that apes use communicative intention to inform their understanding; subjects do not moderate their choices or searches based on ostensive cues. As discussed in Chapter 2, however, most of these experiments share certain practical weaknesses, including the declarative nature of the intended message, the use of pointing or other human-trained reporting behaviours, and the sometimes opaque purpose of the experimental task from the subject's point of view. It is plausible, therefore, that non-human primates' capacity for ostension has not been adequately assessed in an experimental setting, and there is a strong case for further investigation using methodology not directly derived

from tasks used with human infants. Drawing on my dissection of communicative intention and informative intention in Chapter 3, I now return to the question of ostension in primates, and examine whether there are bottom-up methods by which to assess comprehension of communicative intention, derived from naturally occurring animal behaviours.

There is an important relationship between gaze and communication, one that has been highlighted in human and non-human primate literature alike (Argyle et al., 1976; Emery, 2000; Tomasello et al., 2007). Gaze is critical for obtaining and assessing access to another's attention, for coordinating social activities such as play, and for gathering information about the social intentions of others. It has been suggested that the white sclera in human eyes (and genetic variation in primates in which some white is visible in the sclera of certain individuals and certain species) are linked to enhanced communicative gaze-signalling and increased cooperative activity, suggesting that proficient use and following of gaze is an important factor in cognitively complex social interactions (Mayhew & Gómez, 2015; Mearing et al., 2022; Kano, 2022; Kano et al., 2022). Moreover, gaze itself can express communicative intention, if it used not only to access another's attention, but also to intentionally direct it toward an external stimulus. This distinction between the attention-getting and attention-directing functions of gaze was the foundational premise for the first work on ostension in non-human primates, in which observational accounts of enculturated gorillas using their gaze to direct human caregivers' attention toward desired objects led to the suggestion that great apes can engage in ostension using eye gaze (Gómez, 1994, 1996).

Many primate species across several taxonomic groups have been shown to follow the gaze of humans and/or conspecifics, whether the gaze be directed toward a specific spatial location or a specific object. Evidence from great apes (e.g., Barth et al., 2005; Call et al., 1998; Itakura, 1996), Afro-Eurasian monkeys[6] (e.g., Emery et al., 1997; Ferrari et al., 2000; Tomasello et al., 1998), monkeys of the Americas[7] (Amici et al., 2009), prosimians (Ruiz et al., 2009), and callitrichids (Burkart & Heschl, 2006) suggests that primate gaze-following is innate, widespread, and can sometimes be used to acquire information about the location of target objects. Existing gaze-following evidence notes that there are species differences and a developmental age curve in subjects' ability to use gaze to acquire information from others (e.g., Ferrari et al., 2000; Kaplan & Rogers, 2002; Amici et al., 2009). Two potential underlying cognitive mechanisms have been proposed to explain patterns of gaze-following in humans and non-human primates: the orientating-response model and the perspective-taking model. The orienting-response model suggests that individuals across species reflexively orient their gaze in the same direction as others' gaze, without engagement with the purpose or contents of that gaze. Evidence for this model includes findings that various subjects, even adult humans, reflexively follow gaze, even when it has been demonstrated that it will not be predictive of information (Driver et al., 1999; Friesen & Kingstone, 1998). The perspective-taking model of gaze-following proposes that individuals follow gaze because they expect the gaze to have contents (i.e., to contain information), which they themselves can acquire by following the gaze. Evidence for this model includes findings that human and non-human subjects will move their bodies to follow gaze around barriers, rather than simply orienting in the direction of the barrier (e.g., Amici et al., 2009; Bräuer et al., 2005), and that subjects can use gaze to guide their searches for target objects. Instances of "double looks," in which the subject follows gaze to a spatial location, returns to a neutral gaze, and then produces a second look to the same location, have also been cited as potential

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[6] Previously referred to as "old-world monkeys" (Cercopithecidae)
[7] Previously referred to as "new-world monkeys" (Ceboidea)

evidence of perspective-taking, where the expectation of information in the gaze has been violated, if there is nothing relevant in the target location (Call et al., 1998; Bräuer et al., 2005; see also Scerif et al., 2004 for a similar violation-of-expectation paradigm). This model has also proposed that the perspective-taking mechanism may develop ontogenetically, where infant subjects follow gaze using the orienting-response and develop an understanding of the informational relevance of gaze over time.

If the perspective-taking model is an accurate characterization of the cognitive mechanisms underlying gaze-following, then gaze is a valuable measure of sensitivity to ostension in non-human primates. When individuals ascribe contents to others' gaze, gaze-following can be taken as a proxy for the expectation of information, and changes in gaze-following behaviour can be used to assess factors which may influence that expectation of information, such as ostensive behaviour. The importance of gaze as a signal for communicative intention is highlighted in relevance theory (Wilson & Sperber, 2002), where gaze can signal address and can be used to highlight relevant features of the environment for interpretation. Likewise, gaze-following was proposed as a proxy for the expectation of relevant information generated by natural pedagogy (Senju & Csibra, 2008), where human infants were found to follow gaze more often when it was preceded by ostensive signals. There is some criticism of the empirical presumption of a relationship between gaze-following and comprehension of communicative intent, given that gaze does not have to be preceded by ostensive cues in order for subjects to follow it (Gredebäck et al., 2018), and is not, therefore, an absolute measure of communicative expectations, but this does not preclude the use of gaze-following as a proxy for expectation of information if it can be enhanced by ostensive behaviour.

The current study is designed to investigate sensitivity to ostension in non-human primates using gaze-following as a measure of comprehension of communicative intention. In this experiment, I compare the gaze-following behaviour of seven primate species in response to upward looks produced by me, a human experimenter. This experiment is inspired by the method used by Bräuer et al. (2005), who investigated gaze-following between upward-looking and forward-looking conditions, but includes factors which may further moderate gaze-following behaviour. I prime subjects with a behavioural display preceding each upward look: either a display with ostensive, communicative signals, a display that is attention-getting, but not communicative (consuming a piece of food in front of the subject; see Kano et al., 2018), or a time-matched control display with no priming behaviours. The control condition provides a baseline for gaze-following, from which to measure any increase induced by ostension, given that primates do not necessarily need ostensive cues in order to follow gaze. This design also controls for the attention-enhancing quality of ostensive behaviour, to determine whether the communicative nature of the signals, and not merely the attention-grabbing element, is driving any change in response. This paradigm follows both relevance theory and natural pedagogy in terms of its definition of ostension, in which communicative behaviour, addressed to the subject, should trigger a presumption that relevant information will follow. If subjects are sensitive to the informational nature of ostensive communication, then the ostensive display (expression of communicative intention) will increase their expectation of information, and, when paired with an upward look, will increase the expectation that the upward location should contain relevant contents. Specifically, the current study measures the occurrence of double looks during gaze-following, which, according to the perspective-taking model, reflect defied expectation of information.

This design addresses some of the limitations I have highlighted from previous work on ostension in primates. First, it uses a widespread and naturally occurring response variable, as opposed to a trained behaviour such as pointing, which may decrease the cognitive load of each trial and will reduce any pre-existing biases or learned associations that may arise from behavioural training. Similarly, the informative signal from the human experimenter is one that primates experience in their natural ontogeny – gaze – as opposed to a behaviour they experience only with human caregivers, such as pointing. Second, the food rewards in this paradigm are used only to hold the attention of the subject and will not be contingent on their behaviour; any emerging patterns indicating sensitivity to ostension will not be shaped, rewarded, or solicited by the experimenter. Third, this paradigm does not require that the subjects acquire declaratively shared information. Kano et al. (2018) found that ostensive signals enhanced overall gaze-following in apes, more so than attention-getting displays, but not specifically toward target objects, suggesting that the disconnect may be in acquiring the declarative message. This design does not contain a specific message (such as the relevance of a specific, arbitrary target object) that the subjects must interpret in order to report comprehension of ostension – they only need to form an expectation of information, which is then defied. Finally, this study requires no prerequisite training and no apparatus apart from a means of delivering food rewards and can therefore be conducted in a range of settings with many primate species, including research-naïve individuals. This experiment can thus include subjects of diverse rearing histories and varied experience with cognitive research, which helps smooth out effects of variation in husbandry practices, past research experience, and social group organization.

The purposes of this investigation are twofold. First, this study is designed to validate and expand evidence for the perspective-taking model of gaze-following, especially the evidence found in Bräuer et al. (2005): instances of double looks, which occur on a developmental age curve. Second, this study investigates sensitivity to ostension, controlling for the effect of increased attention, where gaze-following functions as a measure of expectation of information. If subjects' gaze-following is moderated by ostension, this is compelling evidence that they ascribe informational contents to gaze, and the perspective-taking model is an appropriate characterization of the cognitive mechanism underlying this behaviour. The predictions of this study are as follows: first, as a manipulation check, the rate of attention during the displays and subsequent upward looks should be equivalent between the ostension and attention-getting conditions, to demonstrate that the attention-getting display is an adequate control for the attention-getting nature of ostensive signals. Second, if subjects are sensitive to ostension, and the ostensive display therefore increases their expectation of information from the experimenter's upward gaze, they will produce more double looks on ostension trials than on attention-getting or control trials, reflecting their defied expectations. If subjects are sensitive to the communicative relevance of ostension, but attention accounts for a portion of that effect, then a pattern may emerge in which the rate of double looks varies significantly between all three conditions, with ostension inducing the highest rate of double looks, but with attention-getting trials showing an elevated rate from the control baseline. If attention is the only driver of increased double looks, then the ostension and attention-getting conditions should induce equivalently higher rates of double looking from the baseline. Finally, if double looks reflect a defied expectation of information, they will occur at higher rates in juvenile and adult subjects, compared to infants, in line with previous findings regarding the developmental curve of the perspective-taking model of gaze-following.

Methods

Subjects

Subjects for this study included 71 individuals across 7 primate species: 5 orangutans (*Pongo pygmaeus*), 6 gorillas (*Gorilla gorilla*), 10 bonobos (*Pan paniscus*), 19 chimpanzees (*Pan troglodytes*), 3 siamang gibbons (*Symphalangus syndactylus*), 3 buff-cheek gibbons (*Nomascus gabriellae*), and 25 brown capuchin monkeys (*Sapajus apella*). Subjects' ages ranged from 1-56 years and were classified into age groups following Bräuer et al. (2005) for great apes, Geissmann (1991) for gibbons, and Fragaszy et al. (2004) for capuchins: *infant* (great apes: 0-4 years; gibbons: 0-2 years; capuchins: 0-1 years); *juvenile* (great apes: 5-10 years; gibbons: 3-5 years; capuchins: 2-5 years); and *adult* (great apes: 10+ years; gibbons: 6+ years; capuchins: 6+ years). All subjects were housed in social groups with conspecifics, across two zoo locations (orangutans, gorillas, bonobos, siamangs, and 8 chimpanzees at Twycross Zoo, England, UK; buff-cheeks, capuchins, and 11 chimpanzees at RZSS Edinburgh Zoo, Scotland, UK). All subjects' enclosures included access to both indoor and outdoor areas, with food, water, and enrichment available ad libitum. Subjects varied in rearing history and were classified as follows: *wild* (subject born and reared throughout infancy in a wild environment); *hand-reared* (subject was reared exclusively by or had extensive contact with human caregivers); and *parent* (subject was reared in captivity by parent and other conspecific individuals, or parent-reared with minimal assistance from human caregivers). The capuchins and the chimpanzees at Edinburgh Zoo have had several years of prior experience with interactive cognitive research of this nature, but the buff-cheek gibbons at Edinburgh Zoo and all subjects from Twycross Zoo had no prior experience with face-to-face cognitive research conducted by a human experimenter. **See Table 4.1 for detailed subject demographics.** [8]

Table 4.1 Subject demographic information

Name	Species	Age (Group)	Sex	Location	Rearing History	Prior Research Experience
Kibriah	Orangutan	44 (adult)	F	Twycross Zoo	Hand-reared	No
Maliku	Orangutan	27 (adult)	F	Twycross Zoo	Parent	No
Batu	Orangutan	32 (adult)	M	Twycross Zoo	Parent	No
Kayan	Orangutan	4 (infant)	F	Twycross Zoo	Parent	No
Basuki	Orangutan	4 (infant)	M	Twycross Zoo	Parent	No
Biddy	Gorilla	47 (adult)	F	Twycross Zoo	Wild	No
Asante	Gorilla	36 (adult)	F	Twycross Zoo	Hand-reared	No
Ozala	Gorilla	27 (adult)	F	Twycross Zoo	Parent	No
Oumbi	Gorilla	29 (adult)	M	Twycross Zoo	Parent	No
Lope	Gorilla	8 (juvenile)	M	Twycross Zoo	Parent	No
Shufai	Gorilla	4 (infant)	M	Twycross Zoo	Parent	No
Diatou	Bonobo	44 (adult)	F	Twycross Zoo	Hand-reared	No
Lina	Bonobo	36 (adult)	F	Twycross Zoo	Parent	Unknown
Cheka	Bonobo	25 (adult)	F	Twycross Zoo	Parent	No
Maringa	Bonobo	23 (adult)	F	Twycross Zoo	Parent	No
Likemba	Bonobo	12 (adult)	F	Twycross Zoo	Parent	Unknown
Malaika	Bonobo	11 (adult)	F	Twycross Zoo	Parent	No
Lucuma	Bonobo	19 (adult)	M	Twycross Zoo	Parent	Unknown
Lopori	Bonobo	9 (juvenile)	F	Twycross Zoo	Hand-reared	No

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[8] This study was conducted with ethical approval from the University of St. Andrews School of Psychology and Neuroscience Ethics Committee (see **Appendix G**).

Ndeko	Bonobo	6 (juvenile)	M	Twycross Zoo	Parent	No
Rubani	Bonobo	5 (juvenile)	M	Twycross Zoo	Parent	No
Tango	Siamang	27 (adult)	F	Twycross Zoo	Parent	No
Denzel	Siamang	11 (adult)	M	Twycross Zoo	Parent	No
Darwin	Siamang	8 (adult)	M	Twycross Zoo	Parent	No
Coco	Chimpanzee	56 (adult)	F	Twycross Zoo	Wild	No
Josie	Chimpanzee	33 (adult)	F	Twycross Zoo	Hand-reared	No
Genet	Chimpanzee	26 (adult)	F	Twycross Zoo	Hand-reared	No
Tuli	Chimpanzee	14 (adult)	F	Twycross Zoo	Parent	No
William	Chimpanzee	39 (adult)	M	Twycross Zoo	Hand-reared	No
Flyn	Chimpanzee	35 (adult)	M	Twycross Zoo	Hand-reared	No
Tommie	Chimpanzee	26 (adult)	M	Twycross Zoo	Hand-reared	No
Kibali	Chimpanzee	17 (adult)	M	Twycross Zoo	Parent	No
Lucy	Chimpanzee	43 (adult)	F	RZSS Edinburgh Zoo	Parent	Yes
Eva	Chimpanzee	39 (adult)	F	RZSS Edinburgh Zoo	Parent	Yes
Sophie	Chimpanzee	38 (adult)	F	RZSS Edinburgh Zoo	Hand-reared	Yes
Kilimi	Chimpanzee	27 (adult)	F	RZSS Edinburgh Zoo	Parent	Yes
Edith	Chimpanzee	24 (adult)	F	RZSS Edinburgh Zoo	Parent	Yes
David	Chimpanzee	45 (adult)	M	RZSS Edinburgh Zoo	Parent	Yes
Louis	Chimpanzee	44 (adult)	M	RZSS Edinburgh Zoo	Wild	Yes
Qafzeh	Chimpanzee	28 (adult)	M	RZSS Edinburgh Zoo	Parent	Yes
Frek	Chimpanzee	26 (adult)	M	RZSS Edinburgh Zoo	Parent	Yes
Liberius	Chimpanzee	21 (adult)	M	RZSS Edinburgh Zoo	Parent	Yes
Velu	Chimpanzee	6 (juvenile)	M	RZSS Edinburgh Zoo	Parent	Yes
Leah	Buff-Cheek[*]	19 (adult)	F	RZSS Edinburgh Zoo	Parent	No
Jon	Buff-Cheek	21 (adult)	M	RZSS Edinburgh Zoo	Parent	No
Donnie	Buff-Cheek	8 (adult)	M	RZSS Edinburgh Zoo	Parent	No
Junon	Capuchin	20 (adult)	F	RZSS Edinburgh Zoo	Parent	Yes
Sylvie	Capuchin	17 (adult)	F	RZSS Edinburgh Zoo	Parent	Yes
Pedra	Capuchin	12 (adult)	F	RZSS Edinburgh Zoo	Parent	Yes
Rosa	Capuchin	10 (adult)	F	RZSS Edinburgh Zoo	Parent	Yes
Luna	Capuchin	9 (adult)	F	RZSS Edinburgh Zoo	Parent	Yes
Alba	Capuchin	9 (adult)	F	RZSS Edinburgh Zoo	Parent	Yes
Hazel	Capuchin	7 (adult)	F	RZSS Edinburgh Zoo	Parent	Yes
Pixie	Capuchin	7 (adult)	F	RZSS Edinburgh Zoo	Parent	Yes
Diego	Capuchin	18 (adult)	M	RZSS Edinburgh Zoo	Parent	Yes
Kato	Capuchin	15 (adult)	M	RZSS Edinburgh Zoo	Wild/Hand-reared	Yes
Toka	Capuchin	15 (adult)	M	RZSS Edinburgh Zoo	Parent	Yes
Figo	Capuchin	14 (adult)	M	RZSS Edinburgh Zoo	Parent	Yes
Carlos	Capuchin	14 (adult)	M	RZSS Edinburgh Zoo	Parent	Yes
Mekoe	Capuchin	12 (adult)	M	RZSS Edinburgh Zoo	Parent	Yes
Chico	Capuchin	11 (adult)	M	RZSS Edinburgh Zoo	Parent	Yes
Inti	Capuchin	11 (adult)	M	RZSS Edinburgh Zoo	Parent	Yes
Ruben	Capuchin	10 (adult)	M	RZSS Edinburgh Zoo	Parent	Yes
Rufo	Capuchin	10 (adult)	M	RZSS Edinburgh Zoo	Parent	Yes
Ximo	Capuchin	10 (adult)	M	RZSS Edinburgh Zoo	Parent	Yes
Flojo	Capuchin	9 (adult)	M	RZSS Edinburgh Zoo	Parent	Yes
Torres	Capuchin	9 (adult)	M	RZSS Edinburgh Zoo	Parent	Yes
Fudge	Capuchin	7 (adult)	M	RZSS Edinburgh Zoo	Parent	Yes
Bear	Capuchin	7 (adult)	M	RZSS Edinburgh Zoo	Parent	Yes
Matoury	Capuchin	1 (infant)	F	RZSS Edinburgh Zoo	Parent	No
Cayenne	Capuchin	1 (infant)	M	RZSS Edinburgh Zoo	Parent	No

*Hybrid buff-cheeked gibbon (Nomascus gabriellae)/white-cheeked gibbon (Nomascus leucogenys)

Materials

I conducted the experiment for all subjects at both locations. For all subjects apart from the Edinburgh chimpanzees, with whom I had worked on previous experiments, I first completed a period of habituation and familiarization with each primate, to ensure that they were

accustomed to my presence and able to engage in basic research procedures such as sitting in front of a feeding tube for 5-10 minutes and accepting food. I tested subjects individually, but for all species apart from capuchins, individuals were not separated for testing, and it was therefore possible for other individuals to observe or interfere with testing. I did not proceed with trials until the testing individual was not interacting with or distracted by conspecifics, and trials were halted and restarted if interrupted by a conspecific.

I conducted testing in designated research rooms (the BRU; Edinburgh: chimpanzees), designated research cubicles ('Living Links to Human Evolution' Research Centre (LL); Edinburgh: capuchins), sleeping areas ("beds") of the primate enclosures (Twycross: orangutans, gorillas, bonobos, chimpanzees, siamangs), or along the outdoor mesh wall of the primate enclosure (Edinburgh: buff-cheek gibbons). See Figure 4.1 for examples of standing and seated testing. See **Appendix B** for details on each testing area.

Figure 4.1 Example of standing (buff-cheek gibbons, lefthand image) or seated (gorillas, righthand image) testing set-up

Regardless of the nature of the testing area, the experimental set-up was as follows: I sat (great apes), or stood (gibbons, capuchins) facing the subject, separated by either a clear polycarbonate panel or by metal mesh. In all arrangements, I was positioned such that there was no more than 60 cm difference in height between my face and the subject's eyes, and my face and eyes were clearly visible to the subject. I provided high-value food rewards (see **Appendix A)** to hold subjects' attention during trials and used a hyper-realistic fake piece of food (replica of high-value food included in subjects' normal diet) for certain trials. For capuchins, I replaced this food replica with a real onion (see procedure below). All trials were videotaped from my perspective, with the camera positioned to look over my shoulder.

Procedure

In this experiment, I followed the gaze-following testing procedure first laid out in Call et al. (1998) and used by Bräuer et al. (2005). In accordance with safety protocols related to COVID-19, I wore a mask and clear face shield during testing, which obscured my nose, mouth, and chin, but did not prevent subjects from observing the position of my head and eyes. In order to test for the effect of ostensive communication on gaze-following behaviour,

I added a display phase to the gaze-following procedure established in Call et al. (1998), in which I produced a communicative (or otherwise) display prior to directing my gaze upward. Trials were divided into three phases, as follows:

Feeding Phase: I fed the subject a set, randomized number of high-value food rewards (between 1 and 4), offering each piece of food in quick succession. On the last food reward of the set number, I did not immediately give it to the subject, but instead held it in front of myself at chest height.

Display Phase: While holding the food reward at chest height, I engaged in one of three displays (each lasting three seconds):

1. Ostensive Communication: I attempted to make eye contact, called the subject's name, and lightly, rhythmically tapped my knuckles against my knees while bouncing my body (seated testing), or waved my hands gently back and forth near my face (standing testing).

2. Attention-Getting, Non-Communication: Without making eye contact or any direct address to the subject, I took a hyper-realistic food replica, briefly pulled down my mask, and within view of the subject, pretended to bite into it, producing a loud chewing sound. I then replaced my mask and placed the prop out of view of the subject once more. Due to restrictions of the testing conditions and safety precautions for COVID-19, this display was not possible with capuchin monkeys. Instead, I produced a species-typical, food-related grooming behaviour: rubbing a real onion against my shoulder and producing an audible rustling noise.

3. Control: I maintained a neutral posture and expression and did not produce any additional behaviours.

Looking Phase: Still holding the food reward at chest height, I oriented my head and eyes to gaze upward for ten seconds.

Immediately following the conclusion of the gazing phase, I gave the food reward to the subject, which began the feeding phase for the next trial. I repeated three phases six times within a single session, for a total of six trials per session. Each display phase appeared twice per session, once in the first three trials and once in the second three trials, with the order of displays counterbalanced within each set of three trials. At the end of the sixth gazing phase, I gave the final food reward to the subject and concluded the session. Subjects received eighteen trials in total, divided across three sessions to reduce the effect of habituation to my upward gaze.

Scoring and Analyses

I coded subjects' behaviour for duration of attention during the both the display and looking phases of each trial, and number of upward looks in the looking phase of each trial. I encoded attention as the total number of seconds (continuous or intermittent) the subject spent with their head and eyes oriented in my direction. I did not consider the position of the subject's body nor any additional behaviours (e.g., grooming, foraging, attempts to reengage the experimenter) with regard to attention, unless the behaviour changed the orientation of the

head or eyes. I defined upward looks as any instance in which the subject oriented their head and eyes upward (above their neutral eyeline). I did not code movements of the eyes alone, absent any head movement; it was not possible to determine the eye position of certain species without movement of the head. I only counted upward looks as separate instances if the subject first returned to a neutral head position (looking neither up nor down) before orienting upward once more. I conducted behavioural coding using BORIS, an open-source event-logging software (Friard & Gamba, 2016).

An additional coder, naïve to the empirical questions and predictions of this study, scored attention and upward looks for 20% of trials. I calculated the intraclass correlation coefficient for the duration of attention and number of upward looks using two-way, absolute-agreement, random-effects models with a 95% confidence interval. Reliability analysis showed generally good agreement (display phase attention, ICC=0.85, CI=0.80-0.90; looking phase attention, ICC=0.79, CI=0.70-0.86; upward looks, ICC=0.71, CI=0.56-0.81).

I transformed attention during the display and looking phases of each trial from the raw number of seconds of attention to the proportion of the phase during which the subject attended to me (such that attention to the display or looking phase of any given trial is a value between 0 and 1). I converted upward looks into a pair of binomial response variables, as follows: initial looks (0 = no upward looks at all, 1=at least one upward look), and double looks (0 = either no upward looks at all or only one upward look, 1 = at least two upward looks). Certain subjects were prone to triple, quadruple, and quintuple upward looks, but these instances were infrequent (N_3=18 trials, N_4=6 trials, and N_5=1 trial), and I did not analyse them as separate response variables, although I included those trials in the rates of initial and double looks (trials in which the subject looked up at least once or at least twice, respectively).

I analysed the effect of display type (ostension, attention-getting, and control) separately for initial and double looks, using generalized liner mixed models (GLMM; Baayen et al., 2008) with a binomial error structure and logit link function (McCullagh & Nelder, 2019). I analysed the effect of display type on attention in the display phase and looking phase using two separate linear mixed models with a gaussian error structure. In all four models, I included display type and subject age group (infant, juvenile, adult) as fixed factors. I scaled session number (1-3) and trial number within session (1-6) to a mean of 0 and a standard deviation of 1 and included them as fixed factors to assess and control for the effect of habituation within and across sessions. I included Subject ID and species as random effects. I made the decision to included species as a random effect, rather than a fixed effect, to control for variation between species on the grounds that there is considerable variation between the sample sizes for different species, which could bias the analysis of interaction effects, and the advice that factors with more than five levels are best included as random effects (Clark & Linzer, 2015). I implemented the models using the "lmer" and "glmer" functions of R package lme4 (Bates et al., 2015). I calculated p-values for individual fixed effects and interaction terms using likelihood ratio tests of the fitted model with and without the relevant term (R function "drop1", Barr et al., 2013).

Following Barr et al. (2013), I initially fitted models with all possible random slope components of fixed effects within subject ID and species, and then pruned them according to whether the model was able to converge with the random slope included, and whether the AIC of the model improved when the random slope was omitted. In each model, I ultimately omitted all random slopes within subject ID and species by these criteria. Similarly, I pruned

interaction terms between fixed effects if they were not significant ($p>0.05$) and did not improve the fit of the model, as determined by the p-value derived from likelihood ratio tests and changes in the AIC of the model. Following this process, I pruned interactions between display type and both age group and session, respectively, from all four models. I assessed multicollinearity by calculating the generalised variance inflation factors of each model with random effects excluded, using the R package car (Fox et al., 2011). There was no concern with multicollinearity in any of the four models (*GVIF*<2 for all factors, see **Appendix D**).

I conducted pairwise comparisons between the display types for each of the four models, using the "glht" function of R package multcomp (Bretz et al., 2016), which examines the differences in effect between levels of the predictor using multiple comparisons of means. I calculated odds ratios (for the binomial models) and estimated marginal mean differences (for the gaussian models) to assess the relative effect size between each pair of levels of the predictor, display type (R package emmeans, Lenth, 2019). I conducted all analysis in RStudio (version 4.2.1, RStudio Team, 2015).

The initial model assessing the effect of display type on double looks, with age category, session number, and trial number within session as fixed factors, and subject ID and species as random factors, showed a trend toward an interaction between trial within session and display type (χ^2=5.20, *df*=2, *p*=0.074). This tendency suggested that the effect of ostension was subject to habituation within a session, while the effect of the other two displays did not change across trials within a session. Given the nature of this interaction, I dropped the second half of each session from analysis. Thus, I fitted the final models for all four response variables to the data from only the first three trials of each session, which contain the first instance of each display type per session (see Figure 4.2).
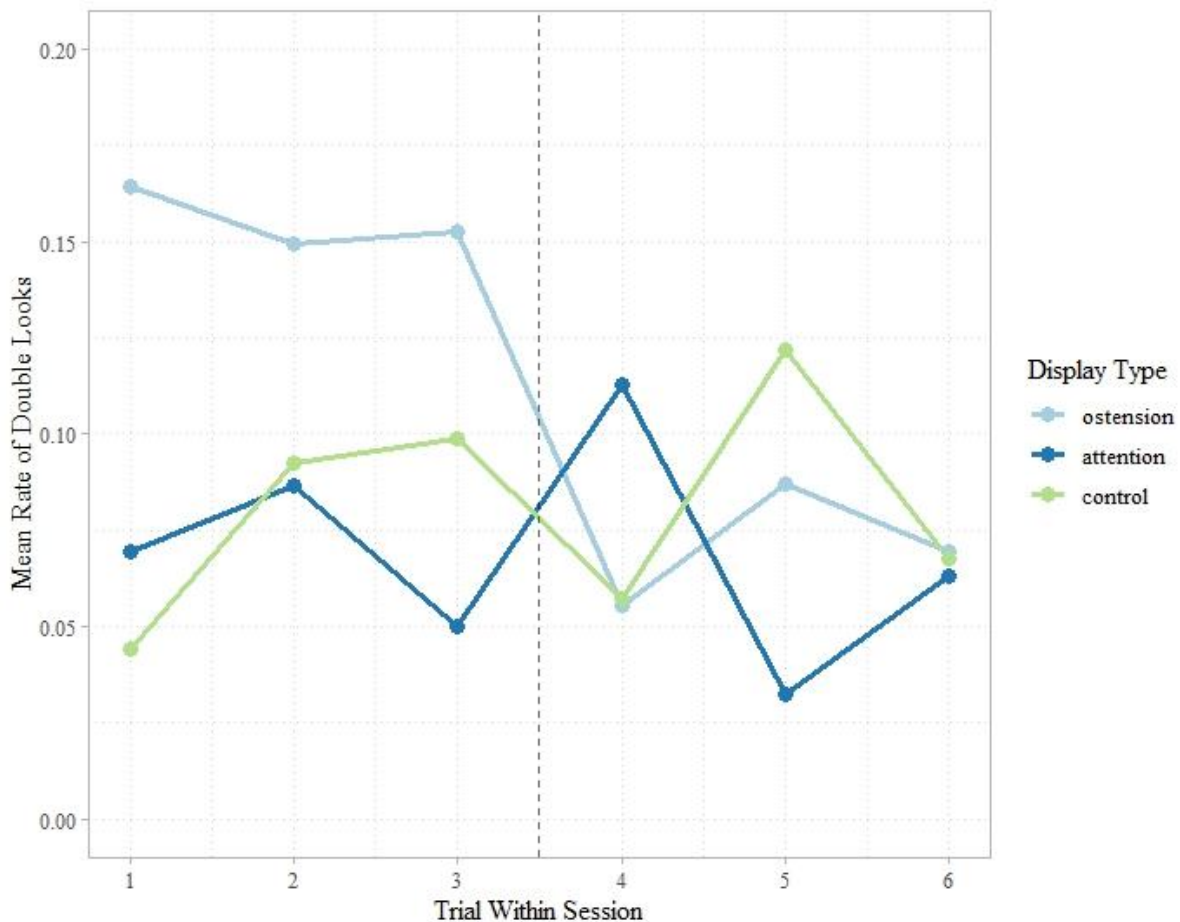
Figure 4.2 Depiction of the interaction between display type and trial number within session (p=0.074). Points represent the mean rate of double looks for each trial within a session, and lines are separated by display type. Given this tendency toward interaction, all subsequent analysis was conducted on only the first three trials of every session, to control for the effect of habituation within sessions (see dashed line).

Results

Attention

Focussing on the first three trials of every session, subjects attended to the experimenter for a mean ($\pm$ SE) of 78% ($\pm$1.2%) of each display phase and 63% ($\pm$1.1%) of each looking phase. There was some variation in duration of attention between age groups and between species, but notably the pattern of attention did not vary between age groups or species: subjects showed a slightly higher proportion of attention to display phases than to looking phases (see Table 4.2 and Table 4.3).

Table 4.2 Mean proportion of attention shown to display phases and looking phases, respectively, separated by age group. Means are displayed with standard error.

Age Group	Display Phase	Looking Phase
infant	0.81 $\pm$ 0.05	0.71 $\pm$ 0.05
juvenile	0.92 $\pm$ 0.04	0.75 $\pm$ 0.03
adult	0.76 $\pm$ 0.01	0.61 $\pm$ 0.01

Table 4.3 Mean proportion of attention shown to display phases and looking phases, respectively, separated by species. Means are displayed with standard error.

Species	Display Phase	Looking Phase
orangutan	0.98 ± 0.02	0.87 ± 0.03
gorilla	0.90 ± 0.04	0.77 ± 0.04
chimpanzee	0.80 ± 0.02	0.63 ± 0.02
bonobo	0.87 ± 0.03	0.73 ± 0.02
siamang	0.75 ± 0.06	0.62 ± 0.05
buff-cheek gibbon	0.80 ± 0.06	0.61 ± 0.04
capuchin	0.66 ± 0.02	0.51 ± 0.02

Display Attention

There was no significant difference in duration of attention between display types (χ^2=3.86, df=2, p=0.145) (see Figure 4.3), or age groups (χ^2=2.15, df=2, p=0.341). Pairwise tests of multiple comparisons of means between display types showed that none of the effects of display types differed significantly from any other (p>0.05 for each pair, see **Appendix D**).
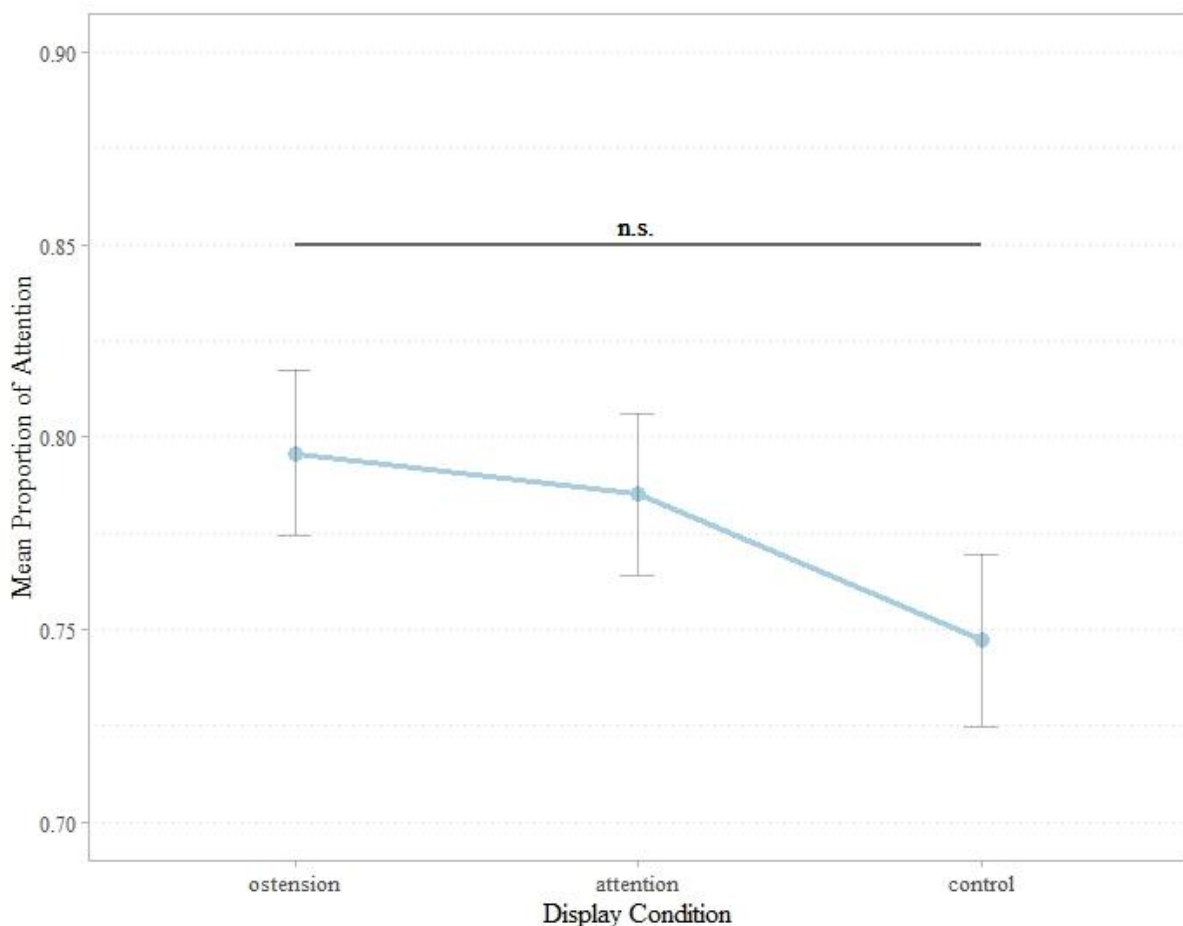
Figure 4.3 Mean proportion of attention in the display phase, separated by display type. Error bars represent standard error of the mean.

Looking Attention

There was also no significant difference in duration of attention between display types (χ^2=1.49, *df*=2, *p*=0.473) (see Figure 4.4), or age groups (χ^2=1.12, *df*=2, *p*=0.568) in the looking phase. Pairwise tests of multiple comparisons of means between display types showed that none of the effects of display types differed significantly from any other (*p*>0.05 for each pair, see **Appendix D**).
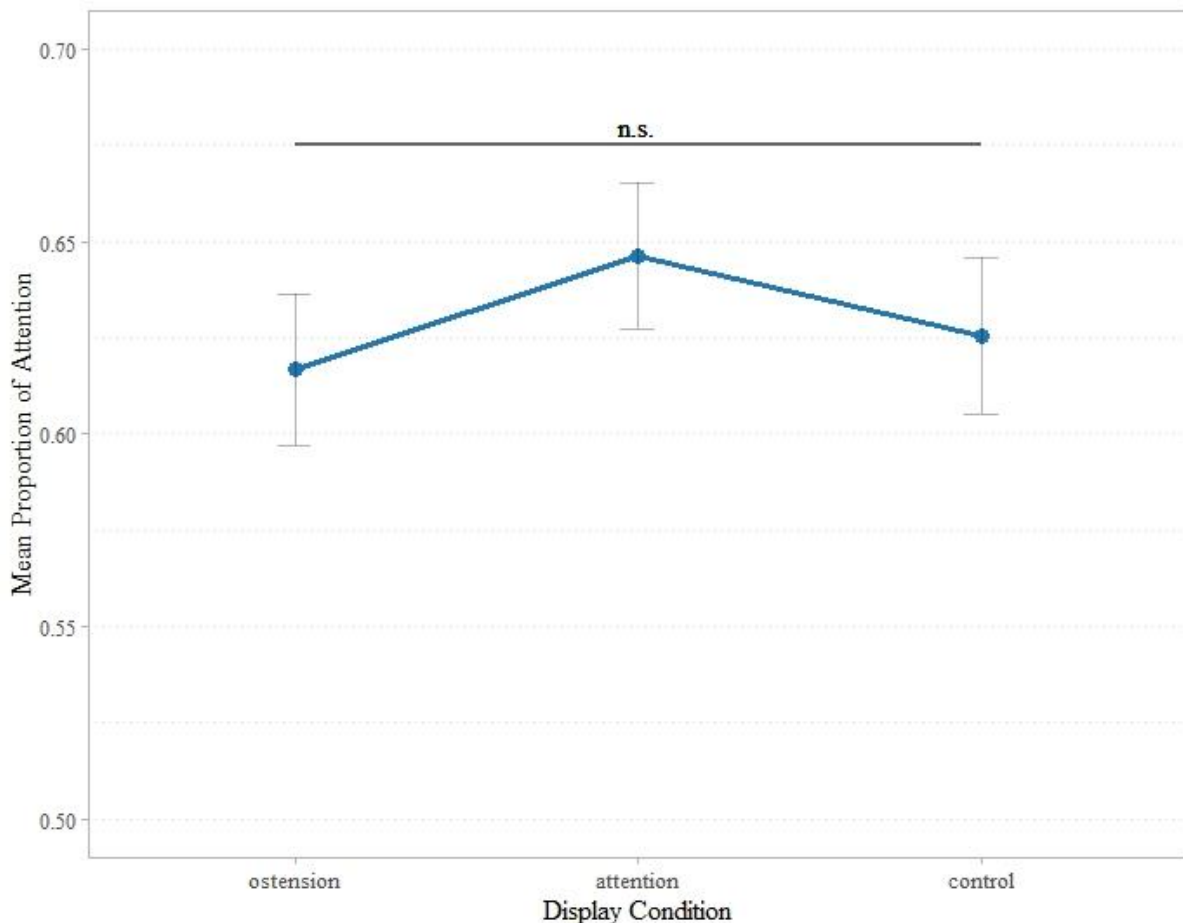
Figure 4.4 Mean proportion of attention in the looking phase, separated by display type. Error bars represent standard error of the mean.

Effect of Session

There was a non-significant trend toward an effect of session on duration of attention in both the display phase (χ^2=3.53, *df*=1, *p*=0.060) and the looking phase (χ^2=2.83, *df*=1, *p*=0.092); subjects showed a tendency toward less attention in later sessions. The interaction between session and display type was not significant for either the display phase or the looking phase; the decrease in attention did not differ between display types in either phase (*p*>0.05 for both phases, see Figure 4.5 and Figure 4.6).
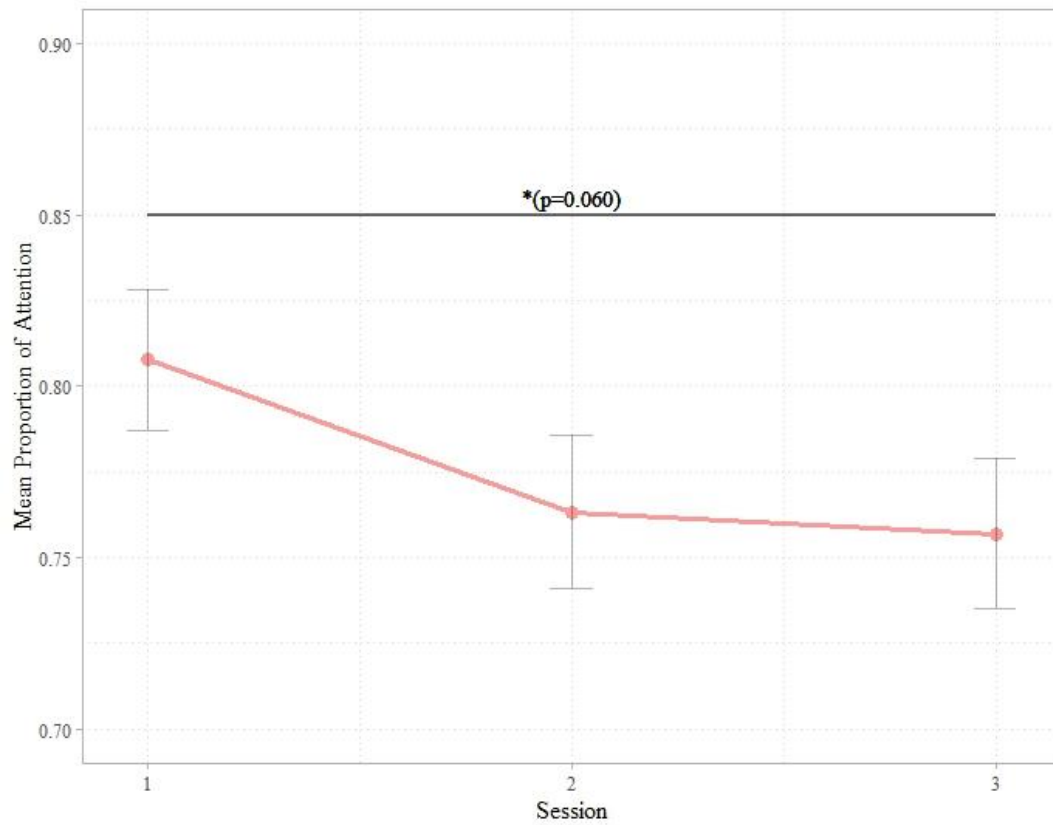
Figure 4.5 Mean proportion of attention in the display phase across sessions. Error bars represent standard error of the mean. *non-significant trend
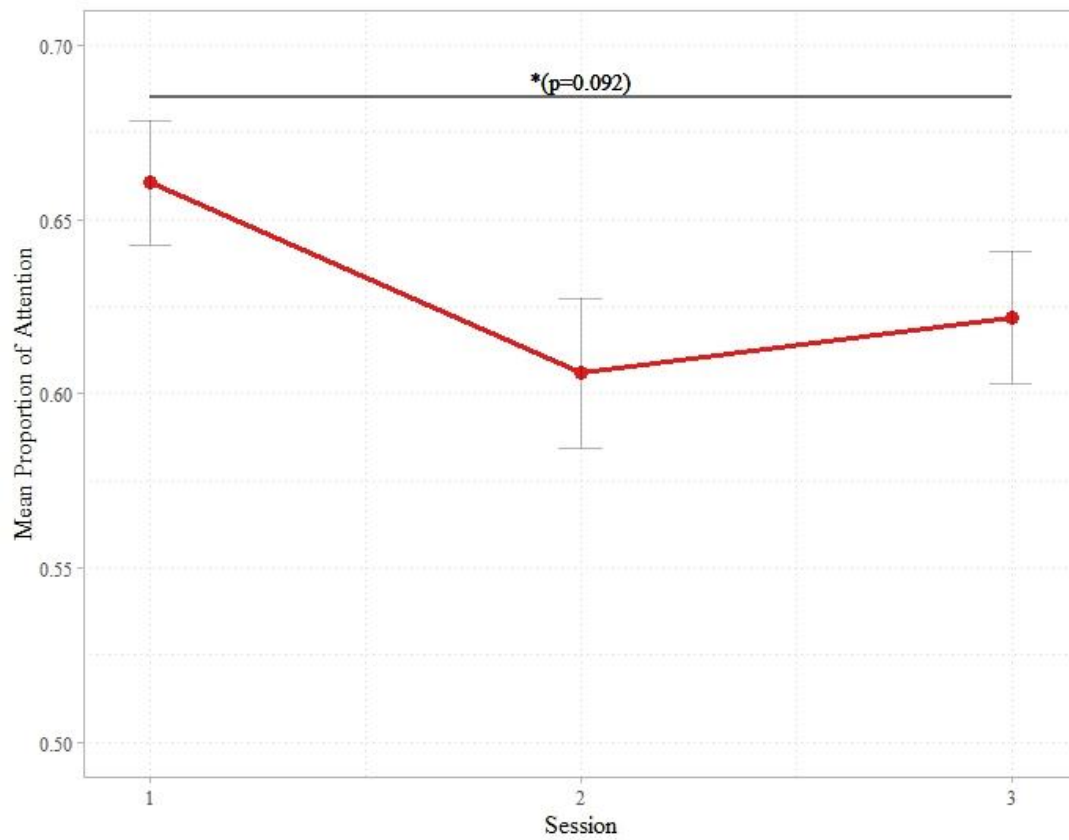
Figure 4.6 Mean proportion of attention in the looking phase across sessions. Error bars represent standard error of the mean. *non-significant trend

Upward Looks

Subjects produced initial upward looks on 37% (±1.9%) percent of trials and double upward looks on 10% (±1.2%) of trials. Overall rates of upward looking varied between age groups and between species (see Table 4.4 and Table 4.5). With regard to age groups, infants produced fewer initial looks, and notably, no double looks at all, while juveniles and adults showed higher rates of both initial and double looks, compared to infants. With respect to species, buff-cheek gibbons showed the highest rate of both initial and double upward looks, followed by bonobos and siamangs. Orangutans showed the lowest rate of initial looks, while gorillas produced the fewest double looks. Species differences are included in the below models as random effects (see Figure 4.7 for a visualization of the effect of display type on mean rate of double looks, separated by species).

Table 4.4 Mean rate of initial and double looks per trial, respectively, separated by age group. Means are displayed with standard error.

Age Group	Initial Looks	Double Looks
infant	0.13 ± 0.05	0.00 ± 0.00
juvenile	0.39 ± 0.07	0.11 ± 0.04
adult	0.39 ± 0.02	0.11 ± 0.01

Table 4.5 Mean rate of initial and double looks per trial, respectively, separated by species. Means are displayed with standard error.

Species	Initial Looks	Double Looks
orangutan	0.24 ± 0.06	0.07 ± 0.04
gorilla	0.32 ± 0.06	0.04 ± 0.03
chimpanzee	0.29 ± 0.03	0.07 ± 0.02
bonobo	0.51 ± 0.05	0.16 ± 0.04
siamang	0.52 ± 0.10	0.11 ± 0.06
buff-cheek gibbon	0.78 ± 0.08	0.44 ± 0.10
capuchin	0.34 ± 0.02	0.08 ± 0.03
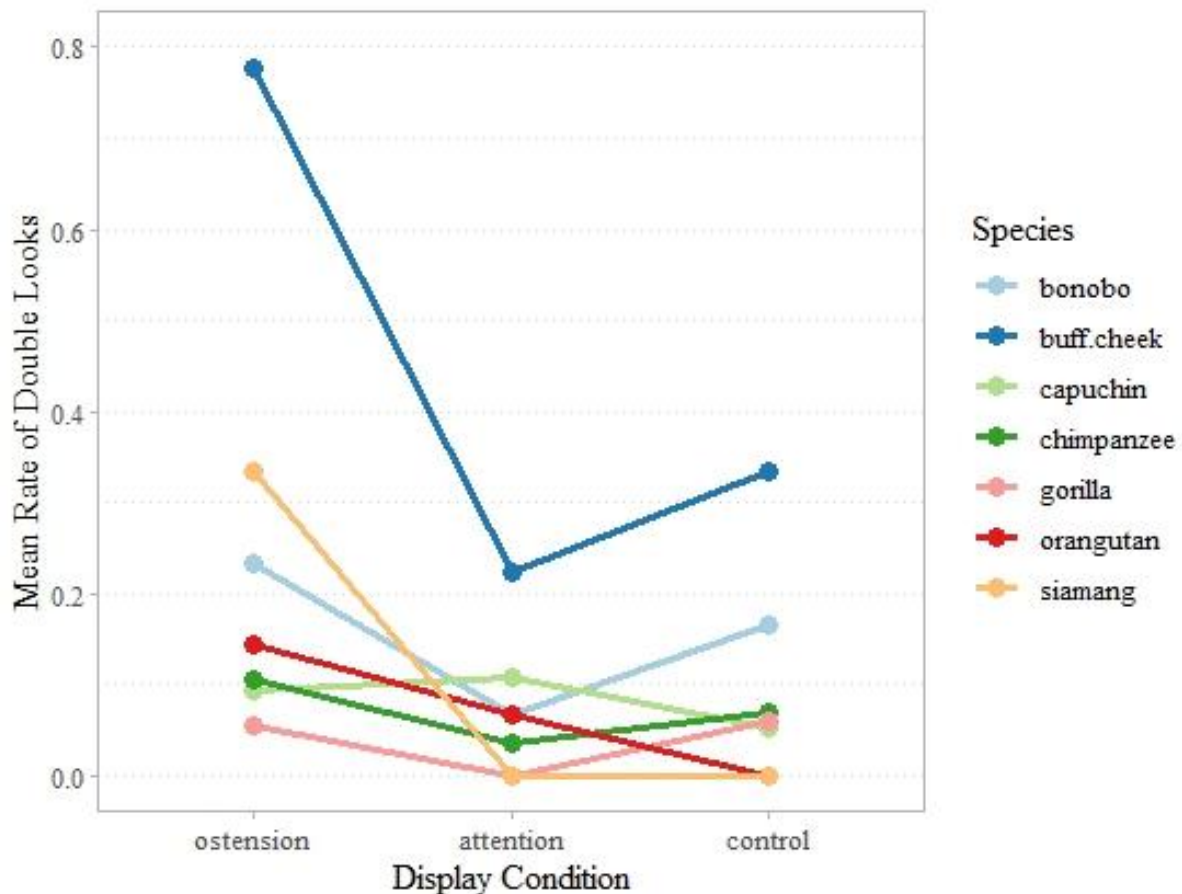
Figure 4.7 The effect of display type on mean rate of double looks, separated by species.

Initial Looks

There was no significant effect of display type on the rate of initial looks; subjects did not moderate their rate of initial looks according to the type of display (χ^2=3.41, *df*=2, *p*=0.182) (see Figure 4.8). Pairwise tests of multiple comparisons of means between display types showed that none of the effects of display types differed significantly from any other (*p*>0.05 for each pair, see **Appendix D**).

Double Looks

There was a significant effect of display type on the rate of double looks (χ^2=10.82, *df*=2, *p*=0.004). Pairwise tests of multiple comparisons of means between display types showed that the ostensive display type resulted in significantly more double looks than either the attention-getting display (*z*=2.82, *df*=1, p=0.013, *OR*=1.62) or the control (*z*=2.48, *df*=1, *p*=0.035, *OR*=1.56). The attention-getting display and the control display did not differ significantly from each other (*z*=0.38, *df*=1, *p*=0.922, *OR*=1.14); subjects produced similar rates of double looks in both (see Figure 4.9). Analysis of odds ratios between display types showed that subjects were 62% more likely to produce a double look on an ostension trial than on an attention-getting trial and 56% more likely than on a control trial. The odds ratio between attention-getting and control trials was comparably smaller; subjects were 14% more likely to produce a double look on a control trial than on an attention-getting trial.
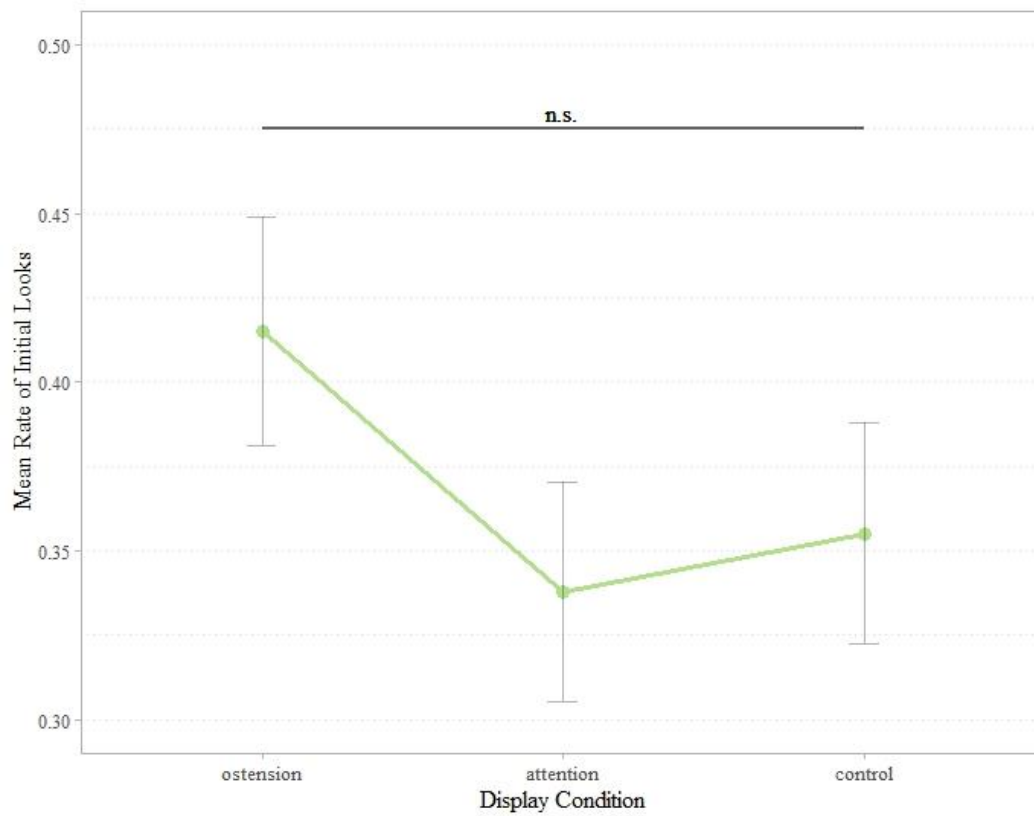
Figure 4.8 Mean rate of initial looks, separated by display type. The error bars represent standard error of the mean.
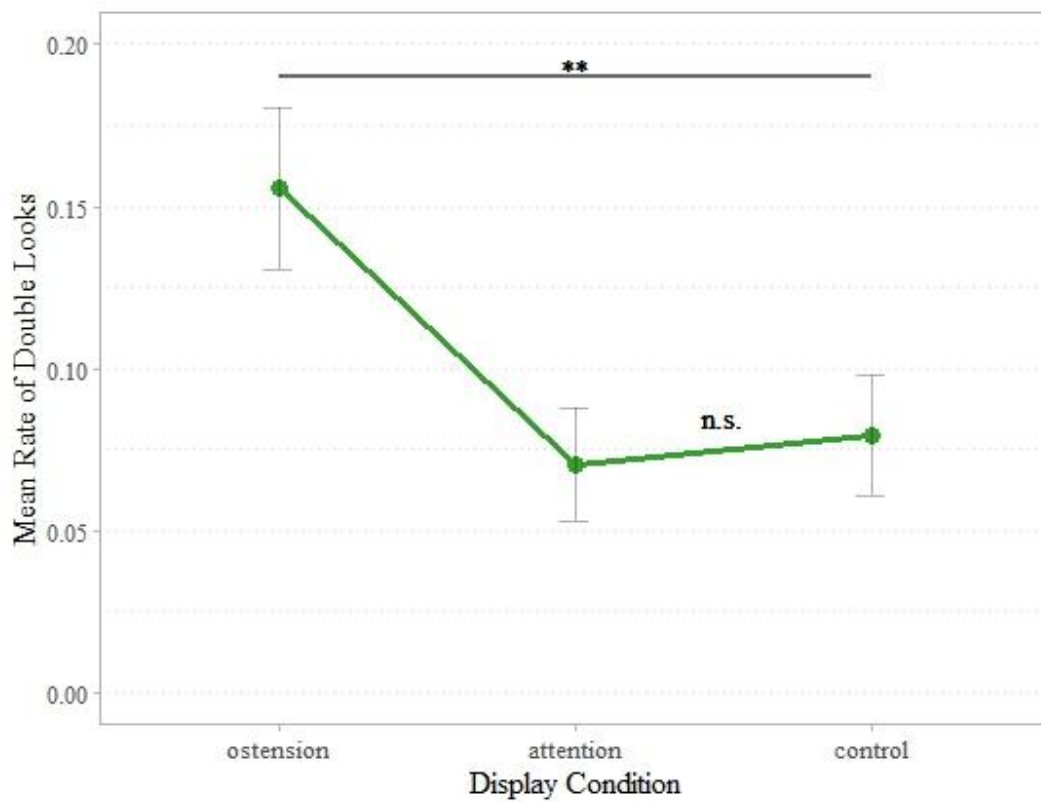
Figure 4.9 Mean rate of double looks, separated by display type. The error bars represent standard error of the mean. **p<0.05

Effect of Age

There was a significant effect of age group in the analyses for both initial (χ^2=6.74, df=2, p=0.034) and double looks (χ^2=8.00, df=2, p=0.018); infants produced fewer initial looks than juveniles and adults, and produced no double looks at all. Juveniles showed similar rates of initial and double looks to those of adults (Figure 4.10 and Figure 4.11). There was no interaction of age group with the effect of display type on either initial or double looks (p<0.05 for both analyses); the effect of age did not differ significantly between display types.
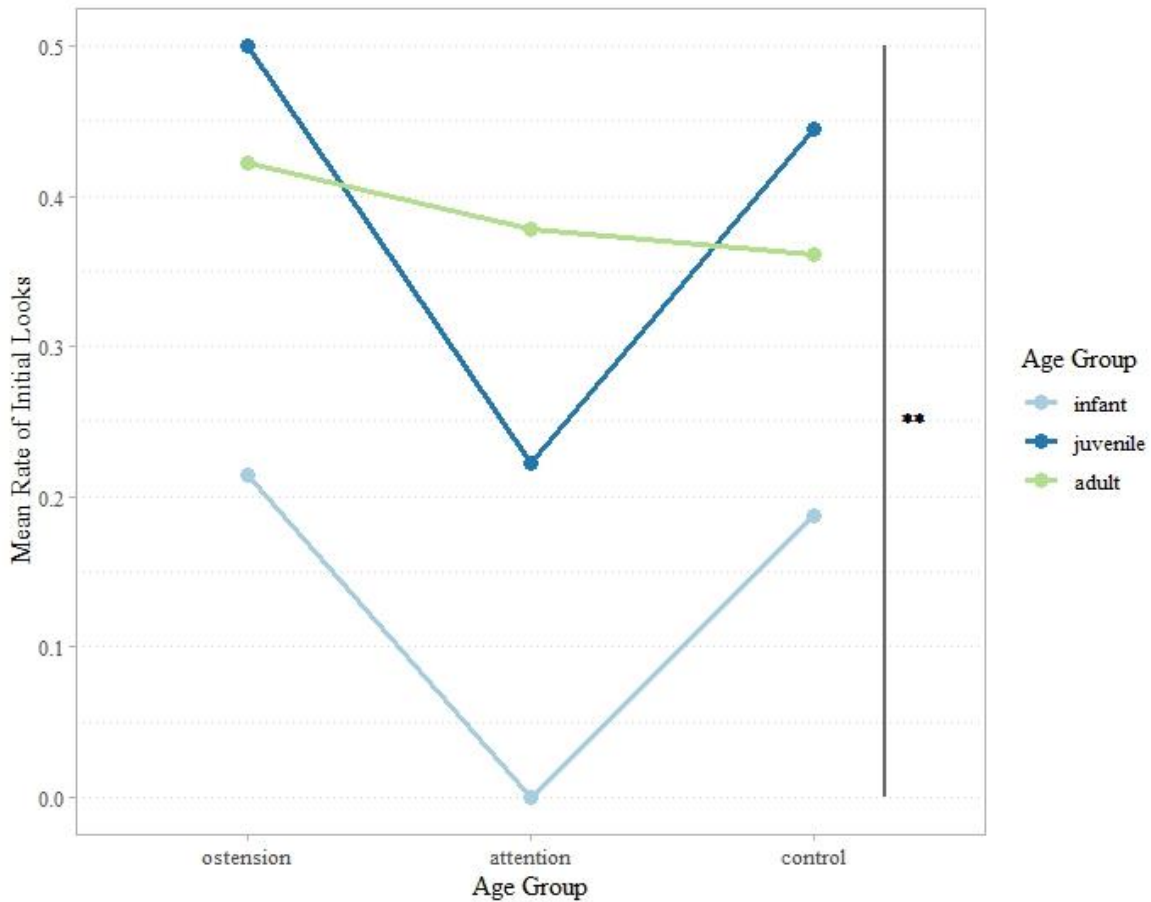
Figure 4.10 Mean rate of initial looks, separated by age group. **p<0.05
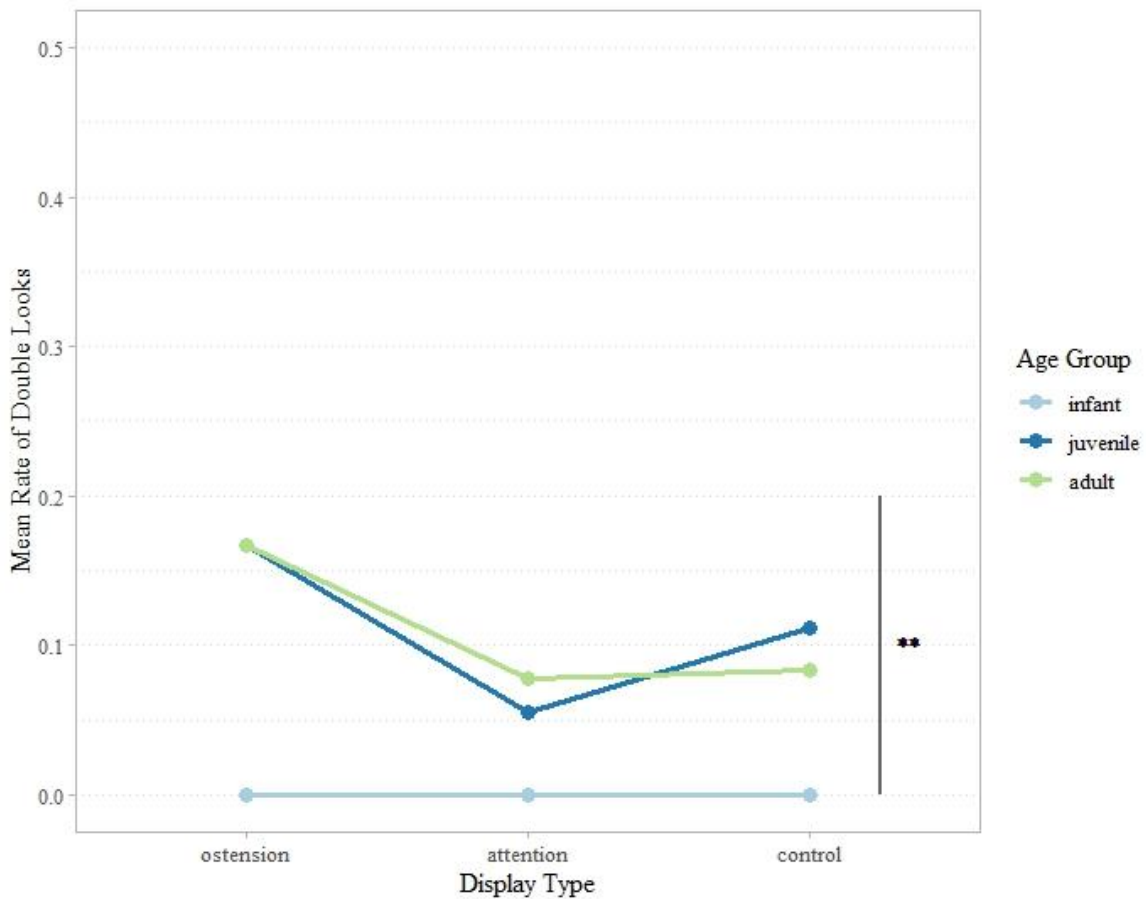
Figure 4.11 Mean rate of double looks, separated by age group. **p<0.05

Effect of Session

There was a significant effect of session in the analyses for both initial (χ^2=5.86, df=1, p=0.015) and double looks (χ^2=11.84, df=1, p<0.001); subjects produced fewer initial looks and fewer double looks across sessions (see Figure 4.12 and Figure 4.13). The interaction between session and display type was not significant for initial or double looks; the overall decrease in rate of looking did not differ between display types (p<0.05 for both analyses).
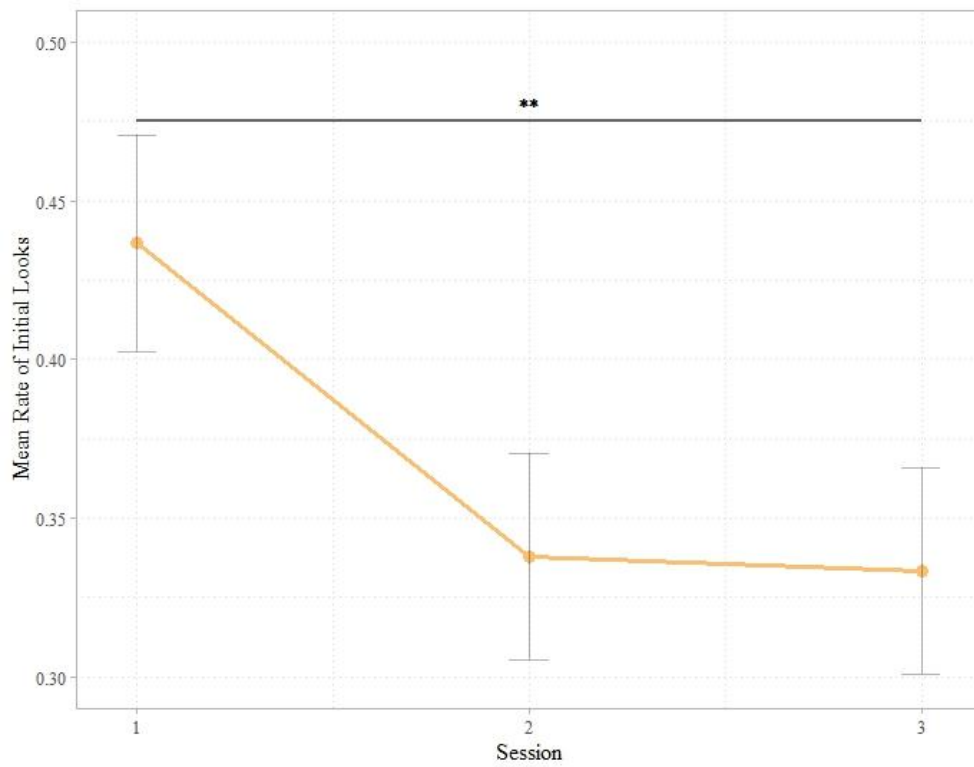
Figure 4.12 Mean rate of initial looks across sessions. The error bars represent standard error of the mean.
***p<0.05*
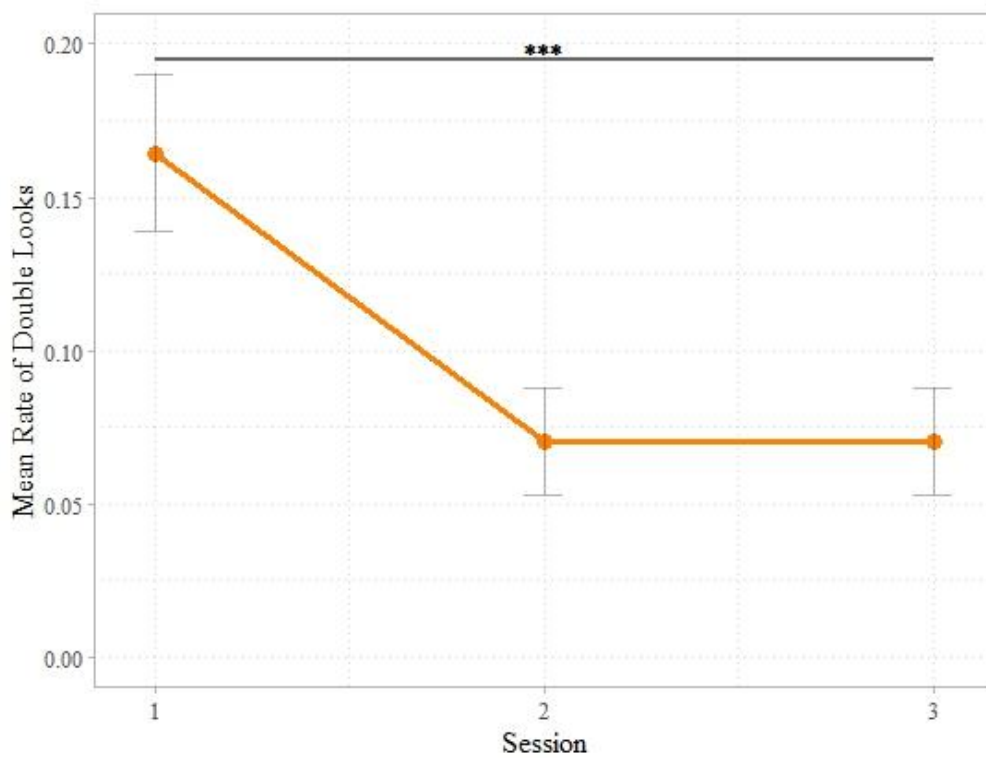
Figure 4.13 Mean rate of double looks across sessions. The error bars represent standard error of the mean.
***p<0.001*

Discussion

The data from this experiment supports my hypothesis that primates' expectation of information can be modified with ostensive behaviour, and that this effect is not driven by enhanced attention. Subjects' proportion of attention to both the display and looking phases of each trial did not vary between display types, suggesting that the ostensive display was no more attention-getting than the attention display. Furthermore, the lapse in feeding appeared to be a stronger driver of attention than any specific behaviour of the experimenter, given that both displays garnered equivalent attention to that induced by the control display. This finding is also supported by the fact that the rate of initial looks did not vary between display types. This experiment found a similar rate of initial looks (37%) to the rate of initial upward looks on upward gaze trials in Bräuer et al. (2005) (44%), the experimental condition of which was similar to the control display in the current experiment. Following the perspective-taking model of gaze-following, my interpretation is that the baseline rate of initial upward looks reflects a baseline expectation that gaze may contain information, which the subject may acquire by following the gaze. The pattern of initial looks also suggests that none of the displays significantly suppressed the rate of looking (for example, forgoing gaze-following to continue to stare at the location where the food prop recently appeared), which might otherwise be a possible explanation for a difference between conditions.

Subjects' rate of double looks was significantly higher following the ostensive display compared to either the attention-getting or the control display, which suggests that the ostensive display alone increased the presumption that the experimenter's gaze should contain relevant informational contents from its baseline, prompting the "double-checking" behaviour when this assumption was violated. The fact that there was no significant difference between the attention-getting and control displays further suggests that this effect is driven primarily by the ostensive, communicative quality of the behaviour, and not by the potentially increased attention to the experimenter.

Subjects showed an effect of habituation toward the experimenter's upward gaze, where their overall rate of gaze-following decreased across sessions. This replicates an effect found by Tomasello et al. (2001), where adult chimpanzees' gaze-following to an empty space diminished over time. Likewise, this experiment replicated the effect of age found in Bräuer et al. (2005), where infants showed lower rates of initial looks, and produce no double looks. These findings support the perspective-taking model of communication; subjects flexibly adjust their looking behaviour based on defied expectations from previous trials, which is contraindicative of the orienting-response model. Similarly, the age curve suggests that gaze-following may begin, ontogenetically, as a reflexive orientating response, and develop over time into a perspective-taking response, as individuals gain a deeper understanding of the nature and purpose of others' gaze.

The increase in double looks following ostensive behaviour also serves as evidence in support of perspective-taking. Given that ostensive behaviour, as a rule, induces an expectation of information in the recipient, and the ostensive display induced a change in the pattern of gaze-following, we can conclude that the gaze-following behaviour is an appropriate measure of expectation of information, which is consistent with the perspective-taking model. These findings also support the suggestion that primates are sensitive to the presumption that communication should contain relevant information, which is triggered by ostension, a key tenant of relevance theory (Sperber & Wilson, 1986). This effect can also be interpreted in keeping with the theory of natural pedagogy (Csibra & Gergely, 2009), in that

the eye contact and addressing function of the ostensive display induced in the recipient an "epistemic trust" (Gergely et al., 2007) that the experimenter was preparing to convey relevant information for them to acquire, more so than the other two displays.

This work found an effect of sensitivity to ostension in primates where some other paradigms, particularly paradigms in which the subject must acquire information about a reward location from a human pointing gesture or behavioural display, have failed to do so (e.g., Chapter 2; Moore et al., 2015; for review, Leavens et al., 2019). There are three key differences between the current paradigm and pointing paradigms that may have contributed to this difference in findings: first, it measures the change in a response behaviour that occurs in the natural repertoire of primates, gaze-following, as opposed to a trained or shaped response behaviour such as pointing to indicate a choice between two objects. Consequently, subjects were not required to invoke any training in order to respond to the stimulus, which may have decreased the cognitive load during trials, compared to pointing paradigms. Second, this paradigm uses a stimulus, gazing, which is widespread in the natural repertoire of many primate species, and which apes experience from conspecifics throughout their ontogenetic development. With the exception of certain enculturated or cross-fostered apes, index finger pointing is not part of the ontogenetic development of social communication between conspecific primates (Tomasello, 2008b). Even if they have experienced pointing from human caregivers, or been trained to point in certain contexts, primates may lack the developmental common ground with humans that would lead them to assume that a pointing gesture is informational. Conversely, primates will have experienced the information-containing nature of gaze in their own social environments and may therefore have been more likely to engage with its meaningful contents, even from a human experimenter. Finally, this paradigm did not demand that subjects actually acquire any specific information, with which they must then report their comprehension via search or choice. Subjects only needed to be surprised that there was no informational contents of the gaze, which they could express without having to convert their interpretation of the experimenter's behaviour into active, sensical choices to find or earn a reward. This non-reward-oriented response variable also had the benefit of bypassing certain search biases, such as a perseverance bias or a gambler's fallacy bias. Taken with the generally underwhelming performance of non-human primates when using a human pointing gesture to obtain information, I propose that the significant effect of ostension in the current experiment is further evidence that pointing paradigms may be a poor tool to detect the capacity for ostension and other communicative processes in non-human primates, rather than a sufficient framework within which to confirm a lack of capacity for ostension.

The design of this study was also advantageous in that it was flexible enough to be applied in multiple research settings without compromising the internal consistency of the experimental manipulation. As a result of this flexibility, and the fact that this design required no specific training and had no minimum passage criterion, I was able to collect a relatively large sample of primates, with multiple species and several populations of research-naïve subjects. The species and experiential diversity of the animals in this sample suggests that the effect of ostension is not unique to one specific population of primates and is therefore not easily explained by experience with specific husbandry routines or pre-existing expectations from other experimental studies.

Although the overall sample size in this study was relatively large, compared to many other zoo-based cognitive studies with primates (see McEwen et al., 2022, for a review of sample size variation in zoo-based primate cognition research), certain species were represented by

only a few individuals, and it is therefore difficult to make inferential predictions about the variation between species in this experimental paradigm. Given the lack of apparatus, lack of prerequisite training, and the short, relatively straightforward procedure in this experiment, this paradigm might be suitable for larger-scale data collection under a framework such as ManyPrimates (a global collective of primate cognition researchers, which is designed to enable the collection of larger and more diverse primate samples using comparable or identical methods in many different sites and species; see ManyPrimates et al., 2019). Such a collaboration could produce a sample with sufficiently large numbers of multiple species to enable direct comparisons between species and a more nuanced look at the relative capacities for ostension in species with different social structures, brain sizes, and environmental pressures. Replicating this study in a collaboration like ManyPrimates would also increase the external validity of the effect if it were indeed still detected in at least some primate species. Given the considerable variation across research sites in housing and husbandry styles, social structures, and individual researchers who would perform the behavioural displays, data collection under ManyPrimates could control for certain confounds that I was unable to control in my study, such as specific nuances of my own behaviour that may have somehow driven the effect.

A limitation in this study was the significant effect of habituation across and within sessions, which resulted in fewer initial and double looks and lower rates of attention in later trials and later sessions. Although this habituation is expected and supports the suggestion that the gaze-following response is more than an orientation-reflex, since it is moderated by past experience in which the expectation of information was defied, it resulted in a relatively low overall rate of looking. In order to increase the number of trials on which an upward look response occurred, and thus increase the potential power of the study in terms of detecting a difference in the pattern of upward looks according to display condition, it would be beneficial to spread the trials and sessions over a longer period of time. Alternatively, a different design could include interspersed trials without an upward look from the experimenter, as in Bräuer et al. (2005), such that subjects are less likely to anticipate the upward look and lose interest in the information it may contain.

This experiment showed that primates' expectation of information can be moderated with ostensive behaviour, suggesting that they are sensitive to the relevant and information-bearing nature of ostensive communication. Several questions stem from this finding, many of which expand on primates' expectations following ostension, and which probe how primates may react to or express their newly modified expectations. First, ostension provokes an expectation of information, but in humans, ostension can also modify the interpretation of subsequent behaviour from the communicating party (as in the theory of natural pedagogy; Csibra & Gergely, 2009). Could an ostensive display moderate, for example, a primate's expectation of action, as it moderated the expectation of information? In order to assess whether the sensitivity to ostension detected in this study is widespread, and not tied uniquely to gazing behaviour, it would be informative to determine whether it can transfer to another type of social interaction, such as a cooperative task. In a related vein, future work could build on the effect found here by examining whether ostension can modify a different behavioural response on the part of the recipient, such as the communicative behaviours that they produce upon receiving the ostension. If primates' sensitivity to ostension is robust, then it should inform their behavioural responses in a range of communicative interactions, and not only in gaze-following. Finally, the effect of ostension could be further explored by examining factors that moderate the effect of the ostension itself, such as the emotional valence of the ostensive display, or the relative subtlety or explicitness with which the

ostension is produced. If subjects are sensitive not only to the presence or absence of ostensive communication in an interaction, but also the variations in the form and functional meanings of the communicative intention, it would go further to suggest that they have some capacity to interpret and apply the flexible and pragmatic nature of ostension in their communicative systems.

Chapter 5 The Effect of Emotional Valence within Ostensive Behaviour on Apes' Expectation of Action

Abstract

In the previous experiment, I found evidence that non-human primates are sensitive to the information-carrying and relevant nature of ostensive communication, and that ostensive displays moderated subjects' expectations of information. The current study was intended to expand this finding by investigating whether sensitivity to ostension is further moderated by the emotional valence of the communication. Emotional valence provides context through which to interpret the informative intention of ostensive communication, and it is critical to take that context into account when assessing primates' comprehension of ostensive displays. This experiment examined whether 38 subjects across all four great ape species moderated their expectation of action based on ostensive communication, and whether they differentiated between two opposite emotional valences to do so. I investigated the effect of positively valenced and negatively valenced ostensive displays, compared to a neutral, non-communicative control, on subjects' expectation of action in a cooperative setting, using their production of impatience and requesting behaviours as a measure. Subjects produced significantly more of these behaviours following the negatively valenced ostensive display, compared to either the positively valenced display or the baseline control. The effect of the positively valenced display did not differ from the control, suggesting that the negatively valenced context alone moderated subjects' expectation of action. I interpret this finding as further evidence that ostension moderates apes' expectations about subsequent interactions, and that this effect cannot be explained by increased attention. While this experiment did find an effect of emotional valence, it is not possible from the current data to determine whether that effect was due to comprehension of the informative intention of the communication, or due to the subject's own resultant emotional state. I discuss the implications of these findings and possible follow-ups to address the limitations on the interpretation of these results.

Introduction

The emotional valence of communicative displays is an important component of ostension, and it is critically under-studied in non-human primates. Investigation into the relationship between emotional context and ostension began with the social biofeedback theory of emotional learning in infants. This model predates the theory of natural pedagogy, but applies similar principles, in which infants learn to differentiate between their own emotional states when their caregivers mirror back "marked," representational displays of the infant's affect, from which the infant learns to generalize emotional "kinds" (Gergely & Watson, 1996). This specific theoretical framework was expanded by Gergely and Király (2019), who wrote that social learning of emotions in humans occurs through the route of natural pedagogy; caregivers ostensively display emotional states as generalisable and culturally relevant, and infants use their sensitivity to ostension to incorporate this information into their understanding of social interactions. Emotional valence has also been oriented within relevance theory (Strey, 2016; Wharton et al., 2021), where authors note that relevance is critical for parsing nuances of emotion in interactions, and also that emotional valence guides the process of comprehension within ostensive exchanges.

There is empirical evidence for the relationship between emotional valence and comprehension of communicative intention in humans; infants make different inferences

about a partner's intentions depending on the emotional context (e.g., Lopez & Walle, 2022). From a theoretical standpoint, the emotional valence of communication may shape the inferences that imbue and compute the meaning of the behaviour. It may also drive behavioural effects that are not directly related to comprehension of communication; emotional valence can act directly on the emotional state of the recipient, which may affect their resultant behaviour whether or not they interpret the information contained in the communication. One criticism of the study presented in Chapter 2, for both the infant and primate iterations, is that the ostensive and non-ostensive displays differed in their emotional valences. Any detectable effect of ostension could therefore have been driven by a resultant change to subjects' internal emotional state, and not their comprehension of the communication. This is a relevant empirical consideration for any investigation of communication that compares the effect of two different behavioural displays – the displays must either be matched in terms of emotional valence, or there must be a control for the effect of emotional context.

The importance of emotional valence in non-human primate communication should not be overlooked. Valence in the form of emotional facial expressions or emotional behaviour has been shown to moderate gaze-following and object choices in primates (Goossens et al., 2008; Buttelmann et al., 2009; for review, see Bard, 2009). There is evidence to suggest that non-human primates express emotion through multiple modalities, including facial expressions, vocalizations, and body language, and that they have some voluntary control over these expressions (Kret et al., 2020). Great apes, specifically, have also been shown to differentiate and correctly match multimodal emotional signals to their correct facial expressions (Parr, 2003). There is a body of work suggesting that apes respond differently to stimuli with varying emotional valences, where negatively valenced stimuli induced response slowing in emotional Stroop tasks (Allritz et al., 2016; Vonk et al., 2022), positively valenced stimuli commanded greater attention then neutral or negative stimuli in bonobos (Kret et al., 2016), and chimpanzees showed enhanced memory of emotionally valenced stimuli compared to neutral stimuli (Kano et al., 2008). Given that emotion plays a role in human interpretation of communicative exchanges, and that primates appear to be sensitive to variations in emotional valence, it is worth investigating whether primates' interpretation of communication is similarly moderated by emotion.

The current study continues the line of inquiry introduced in Chapter 4, and measures sensitivity to ostension in all four great ape species using a naturally occurring and unsolicited behaviour (the non-hominid species included in the previous experiment, gibbons and capuchins, are not included in the current study as a matter of access and availability). This design investigates whether the sensitivity to ostension observed during my gaze-following paradigm is transferrable to a new situation, one which manipulates the subject's expectation of action, rather than their expectation of information. It also explores the impact of emotional valence, directly comparing the effects of differing emotional contexts on subjects' interpretation of communicative behaviour. In this experiment, I establish the expectation that I will, immediately and without prompting, retrieve food rewards for the subject by opening baited containers and giving them the contents. Once this expectation is created within the trial, I interrupt the feeding process with a period of "distraction" in which I stop retrieving rewards and am not responsive to any attempts to reengage my actions. In order to investigate the effect of ostensive communication on expectations of action, and to explore the impact of emotional valence within ostension, I engage in a communicative display with either a positive or a negative emotional valence (or a control display with no communication and neutral valence) prior to the period of distraction. If subjects are sensitive

to the relevance of being addressed with communicative intention, this may moderate their reaction to the lapse in feeding, compared to a baseline reaction in the control condition. The emotional valence of the communication may provide relevant context on which to base the direction of their change in expectations, i.e., if they derive different informative intentions based on emotional tone, it may differentially increase or decrease their expectation of action.

I measure expectation of action in this study using the subject's production of impatience and/or requesting behaviours. As in the gaze-following paradigm, although these behaviours may be provoked by the behaviour of the experimenter (the lapse in feeding, in the current design), they are not solicited by the experimenter, nor are they relevant to the subject's eventual receipt of the reward. While trained and/or solicited responses, such as pointing to choose between objects, may equally be affected by the emotional valence and ostensive nature of the relevant stimuli in a trial, the rate of unstructured, spontaneous requesting behaviours offers a measure of subjects' situational interpretation that is free from shaping and other training biases. All four species of great ape have been observed to produce intentional, goal-directed gestures toward conspecifics, some of which have distinctive imperative functions, such as presenting a body part for grooming, or stroking another's mouth to request food (De Waal, 1988; Pika et al., 2003, 2005; Pika & Mitani, 2006; Liebal et al., 2006; Genty et al., 2009; Hobaiter & Byrne, 2014). Apes also produce a suite of attention-getting and requesting behaviours to request food or other desired husbandry actions from human caregivers, which have been used as a measure of impatience or protest in empirical work (e.g., Call et al., 2004; Hattori et al., 2011; Tempelmann et al., 2011). In this experiment, requesting, and impatience gestures are used interchangeably as measures of expectation of action, as many gestures cannot be assigned solely to one of these purposes based on existing literature, and behaviour may serve more than one of these purposes simultaneously.

In addition to the different emotional valences of the communicative displays, this experiment also includes variation in the type of "distraction" during the lapse in feeding: one in which I am occupied with a tangible task, and one in which there is no apparent cause for my inaction. The difference in the "validity" of my inaction allows this experiment to probe whether subjects produce their requesting behaviours pragmatically based on their perception of my availability. Apes have been shown to differentiate between varying motivations for the same behaviour (or lack of behaviour), such as the distinction between accidental and intentional actions (Povinelli et al., 1998; Call & Tomasello, 1998; Buttelmann et al., 2012) or the difference between an experimenter who is unwilling versus unable to act (Call et al., 2004). If subjects similarly differentiate between distraction types in the current paradigm, it would suggest that they are producing their communication flexibly, and not as an invariable reaction to the lapse in feeding. The two distraction types also differ in terms of access to my visual attention – I do not directly face the ape during the tangible task. Existing research has demonstrated that apes are sensitive to the body, face, and eye gaze direction of humans, and can vary their rate and type of communication accordingly (Kaminski et al., 2004; Liebal, Call, Tomasello, et al., 2004; Tempelmann et al., 2011). These findings, that apes account for the attentional state of the recipient when they make requesting gestures, are also evidence that their production of gestures is flexible and takes the availability of the recipient into account. Replicating that effect here would further indicate that subjects are sensitive to situational differences in communicative interactions, and that their communication varies pragmatically according to the behaviour of the recipient.

The purpose of this study is to expand and elaborate on the finding in Chapter 4, that primates moderate their behaviour based on ostensive communication from a human experimenter. This experiment investigates whether ostensive communication moderates great apes' reactions to a lapse in provision of food rewards, and whether this effect depends on the emotional valence of the ostensive display. If apes are sensitive to the relevance of being addressed by communication, then they should use factors such as emotional valence to inform their expectations about the subsequent interaction. In the context of this study, the purpose of the ostension is to inform the subjects' expectation of continued feeding action from the experimenter. This experiment also investigates the effect of different types of "distraction" from the task at hand (provision of food rewards), juxtaposing different states of the experimenter's practical and attentional availability. In doing so, this experiment assesses whether the impatience and requesting behaviours the apes produce in response to the lapse in the experimenter's feeding actions are flexible and based on the behaviour of the intended recipient, or whether they are rigid and reflexive responses to the cessation in provision of food.

In discussing the predictions of this study, it is important to note that while I expect the emotional valences of the ostensive displays to differentially affect the subjects' expectations of action, I do not expect that my behaviour will decrease their *desire* for action. Thus, if subjects' expectation of action is decreased, but their desire for action remains intact, I expect to see an increase in impatience and requesting behaviours. Conversely, if subjects' expectations of action are increased, then they should produce fewer impatience and requesting behaviours, since they theoretically believe that their goal is about to be met. Thus, the predictions for this study are as follows: first, if ostension moderates subjects' expectations of action compared to the baseline rate of impatience established by the control condition, then their rate of communication will differ significantly from the baseline in one or both ostension conditions. Second, if subjects are sensitive not only to the communicative nature of the ostension, but also the emotional valence of the displays, then their rate of communication should differ between the positively and negatively valenced displays. Specifically, I predict that the positively valenced display will increase subjects' expectation of action, and thus not increase their rate of impatience behaviours, while the negatively valenced display will decrease their expectation of action and thus increase their rate of communication behaviours. Finally, if subjects are sensitive to the nature of my "distraction," I predict that they will produce more communication behaviours in the intangible distraction condition, where my inaction is "invalid" and they do have access to my attention, compared to the tangible distraction condition, where they may perceive my action and my attention as unavailable.

Methods

Subjects

Subjects for this study included 36 individuals across 4 ape species: 5 orangutans (*Pongo pygmaeus*), 5 gorillas (*Gorilla gorilla*), 10 bonobos (*Pan paniscus*), and 16 chimpanzees (*Pan troglodytes*). Subjects' ages ranged from 4-44 years and were classified into age groups following Bräuer et al. (2005): *infant*, 0-4 years; *juvenile*, 5-10 years; and *adult* 10+ years. All subjects were housed in social groups with conspecifics, across two zoo locations (orangutans, gorillas, bonobos, and 8 chimpanzees at Twycross Zoo, England, UK; 11 chimpanzees at RZSS Edinburgh Zoo, Scotland, UK). All subjects' enclosures included access to both indoor and outdoor areas, with food, water, and enrichment available ad

libitum. Subjects varied in rearing history and are classified as follows: *wild* (subject born and reared throughout infancy in a wild environment); *hand-reared* (subject was reared exclusively by or had extensive contact with human caregivers); and *parent* (subject was reared in captivity by parent and other conspecific individuals, or parent-reared with minimal assistance from human caregivers). All subjects in this experiment had first participated in the gaze-following experiment detailed in Chapter 4, and thus had some experience with face-to-face research including behavioural displays by a human experimenter. The chimpanzees at Edinburgh Zoo have had several years of prior experience with interactive cognitive research of this nature, but all subjects from Twycross Zoo had no additional prior experience with face-to-face cognitive research conducted by a human experimenter. **See Table 5.1 for detailed subject demographics. [9]**

Table 5.1 Subject demographic information

Name	Species	Age (Group)	Sex	Location	Rearing History	Prior Research Experience
Kibriah	Orangutan	44 (adult)	F	Twycross Zoo	Hand-reared	Limited
Maliku	Orangutan	27 (adult)	F	Twycross Zoo	Parent	Limited
Batu	Orangutan	32 (adult)	M	Twycross Zoo	Parent	Limited
Kayan	Orangutan	4 (infant)	F	Twycross Zoo	Parent	Limited
Basuki	Orangutan	4 (infant)	M	Twycross Zoo	Parent	Limited
Biddy	Gorilla	47 (adult)	F	Twycross Zoo	Wild	Limited
Ozala	Gorilla	27 (adult)	F	Twycross Zoo	Parent	Limited
Oumbi	Gorilla	29 (adult)	M	Twycross Zoo	Parent	Limited
Lope	Gorilla	8 (juvenile)	M	Twycross Zoo	Parent	Limited
Shufai	Gorilla	4 (infant)	M	Twycross Zoo	Parent	Limited
Diatou	Bonobo	44 (adult)	F	Twycross Zoo	Hand-reared	Limited
Lina	Bonobo	36 (adult)	F	Twycross Zoo	Parent	Limited
Cheka	Bonobo	25 (adult)	F	Twycross Zoo	Parent	Limited
Maringa	Bonobo	23 (adult)	F	Twycross Zoo	Parent	Limited
Likemba	Bonobo	12 (adult)	F	Twycross Zoo	Parent	Limited
Malaika	Bonobo	11 (adult)	F	Twycross Zoo	Parent	Limited
Lucuma	Bonobo	19 (adult)	M	Twycross Zoo	Parent	Limited
Lopori	Bonobo	9 (juvenile)	F	Twycross Zoo	Hand-reared	Limited
Ndeko	Bonobo	6 (juvenile)	M	Twycross Zoo	Parent	Limited
Rubani	Bonobo	5 (juvenile)	M	Twycross Zoo	Parent	Limited
Josie	Chimpanzee	33 (adult)	F	Twycross Zoo	Hand-reared	Limited
Genet	Chimpanzee	26 (adult)	F	Twycross Zoo	Hand-reared	Limited
Tuli	Chimpanzee	14 (adult)	F	Twycross Zoo	Parent	Limited
William	Chimpanzee	39 (adult)	M	Twycross Zoo	Hand-reared	Limited
Flyn	Chimpanzee	35 (adult)	M	Twycross Zoo	Hand-reared	Limited
Tommie	Chimpanzee	26 (adult)	M	Twycross Zoo	Hand-reared	Limited
Kibali	Chimpanzee	17 (adult)	M	Twycross Zoo	Parent	Limited
Lucy	Chimpanzee	43 (adult)	F	RZSS Edinburgh Zoo	Parent	Yes
Eva	Chimpanzee	39 (adult)	F	RZSS Edinburgh Zoo	Parent	Yes
Kilimi	Chimpanzee	27 (adult)	F	RZSS Edinburgh Zoo	Parent	Yes
Edith	Chimpanzee	24 (adult)	F	RZSS Edinburgh Zoo	Parent	Yes
Louis	Chimpanzee	44 (adult)	M	RZSS Edinburgh Zoo	Wild	Yes
Qafzeh	Chimpanzee	28 (adult)	M	RZSS Edinburgh Zoo	Parent	Yes
Paul*	Chimpanzee	27 (adult)	M	RZSS Edinburgh Zoo	Parent	Yes
Frek	Chimpanzee	26 (adult)	M	RZSS Edinburgh Zoo	Parent	Yes
Velu	Chimpanzee	6 (juvenile)	M	RZSS Edinburgh Zoo	Parent	Yes

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[9] This study was conducted with ethical approval from the University of St. Andrews School of Psychology and Neuroscience Ethics Committee (see **Appendix G**).

Materials

I conducted the experiment with all individuals at both zoo locations. I tested each subject individually, but subjects were not separated from groupmates for testing, and it was therefore possible for other individuals to observe or interfere with testing. I did not proceed with trials until the testing individual was not interacting with or distracted by conspecifics, and I halted and restarted trials if interrupted by a conspecific. As in Chapter 4, I conducted testing in designated research rooms (the BRU; Edinburgh), or the sleeping areas ("beds") of the ape enclosures (Twycross). See **Appendix B** for details on each testing area.

Regardless of the nature of the testing area, the experimental set-up was as follows: I sat facing the subject, separated by a metal mesh panel, positioned such that there was no more than 60 cm difference in height between my face and the subject's eyes, and my face and body were clearly visible to the subject. In accordance with safety protocols related to COVID-19, I wore a mask and clear face shield during testing, which obscured my nose, mouth, and chin, but did not prevent subjects from observing the position of my head, body, or hands, nor did they prevent subjects from hearing my voice. I provided high-value food rewards (see **Appendix A**) through a feeding tube attached to the mesh panel (Twycross), or via a slider on top of a table attached to the mesh panel (Edinburgh). I used five small transparent boxes with detachable lids to contain individual pieces of food during portions of the procedure for each trial. These boxes rested on the floor at my feet (Twycross) or on the table in front of me (Edinburgh), were always visible to the subjects; subjects could freely observe whether the boxes were open or closed, and whether they contained a piece of food (boxes always contained a single piece of food when they were closed). All trials were videotaped from my perspective, with the camera positioned to look over my shoulder (see Figure 5.1).

Figure 5.1 Example of testing set-up at Edinburgh Zoo (chimpanzees, lefthand image) and Twycross (orangutans, righthand image)

Procedure

The experiment was designed to create the expectation that I would retrieve the food from each box in quick succession, without prompting, and give it to the subject. In order to test the effect of ostension and emotional valence on this expectation, I interrupted this feeding process with one of three communicative (or control) displays, followed by a period of

"distraction" during which I did not open boxes and retrieve food rewards. Although the words and hand gestures used in these displays may have been used in front of or toward subjects in the past, they received no training in terms of what to expect following each type of display, and none of the words or gestures were formally used in their normal husbandry or normal research routines. As in the gaze-following study (Chapter 4), trials were divided into three phases, as follows:

Feeding Phase: Each trial began with all five boxes closed and baited with one piece of food each. I opened the first box in view of the subject, removed the piece of food, gave it to the subject, and placed the empty box on the floor or table, still open, before proceeding to the next box. After a randomized, counterbalanced number of boxes (between 2-4), I picked up the next box and held it in front of myself but did not immediately open it to retrieve the food reward.

Display Phase: Still holding the box in front of myself, in the location where I would normally open it, I engaged in one of the following three displays (each lasting three seconds), with my head and body oriented toward the subject.

1. Ostensive/Negative - "Wait": I attempted eye contact, held the box in one hand, held out my other hand with one finger extended upright, and said "hold," in a stern, drawn-out tone.

2. Ostensive/Positive- "Invite": I attempted eye contact, held the box in one hand, used my other hand to produce a whole-hand beckoning gesture (as if signalling "come here" to a human), and said "look!" in an excited, drawn-out tone.

3. Non-Ostensive/Neutral - Control: I continued to hold the box in two hands, and did not make eye contact with the subject, nor produce any body or hand movement.

Distraction Phase: Immediately following the display, and still holding the box in front of myself, I engaged in one of two types of "distraction" from my task of retrieving food (each lasting ten seconds).

1. Clipboard: I continued to hold the box in the same position with one hand but turned my head and body to the side and used a pen to write on a clipboard.

2. Still Face: I returned my second hand to the box (if necessary), and kept my head and body oriented forwards, not making eye contact with the subject, with a blank expression and neutral posture.

Immediately after the ten-second period of "distraction," I opened the box I was holding and gave the food reward to the subject. I then baited and closed all five boxes again, in view of the subject, and began the feeding phase of the next trial. This study had a 2x3 within-subjects design, such that each subject received each display (wait, invite, control) + distraction (clipboard, still face) pair 6 times, for a total of 36 trials. I administered trials in blocks 6 trials per session; each display-distraction pair appeared once per block of six trials, in a randomized, counterbalanced order. 34 subjects completed all 36 trials; the remaining 2 subjects were still included in the sample, having completed at least five trials with each display-distraction pair (N_{trials}=30 and 34, respectively).

Scoring and Analyses

I scored subjects' behaviour from video recordings for "communication" behaviours during the both the display and distraction phases of each trial. These behaviours included a mixture of acts commonly used by captive apes to request food or express protest toward humans (see Table 5.2) and were only counted if they were performed in my direction and within one arm's reach of the mesh panel (while I coded these acts as "communication" for the purposes of this ethogram, see Discussion for analysis of whether these behaviours constitute true efforts to communicate). I counted repetitive acts (e.g., nodding, tapping) only once per bout, unless the act fully ceased for at least 1 second before beginning again, or the subject changed the location of the behaviour within the mesh panel. I collated the number of communication behaviours per subject as a raw count, collapsed across behaviour type, for each phase (display, distraction) of each trial. I conducted behavioural coding using BORIS, an open-source event-logging software (Friard & Gamba, 2016).

*Table 5.2 Ethogram of communication behaviours. See **Appendix E** for more detailed criteria for coding these behaviours.*

Behaviour	Definition
tap	the subject taps or raps their fingers or hand against the table, mesh, or feeding tube
finger thrust	the subject thrusts their fingers (or single finger) through the mesh
present mouth	the subject presents their lips or mouth, open or closed, through the mesh
present body	the subject presents a part of the body by pressing it forward against or through the mesh (accepted parts include chest, back, genitals/bum, shoulder, and foot)
head nod	the subject moves their head up and down rapidly and repeatedly (at least two movements)
hand fling	the subject raises their hand upward and produces a flinging gesture toward the shoulder
clap	the subject claps their hands together, either once or repeatedly
tap body	the subject taps their fingers or hand repetitively against their own body
pass object	the subject pushes or holds an object through the mesh (e.g., stick, enrichment items)
grumble	the subject produces an audible, low-pitched vocalization, akin to a grunt, grumble, or cough
raspberry	the subject produces a lip buzzing/raspberry sound
spit	the subject spits water, saliva, or an object in the direction of the experimenter

An additional coder, naïve to the empirical questions and predictions of this study, scored the number of communication behaviours for 10% of trials. I calculated the intraclass correlation coefficient for the number of communication behaviours in each phase using a two-way, absolute-agreement, random-effects model with a 95% confidence interval. Analysis of interobserver reliability showed good agreement (display phase: ICC=0.70, CI=0.57-0.76; distraction phase: ICC=0.88, CI=0.84-0.92).

I analysed the effect of display type (wait, invite, and control) separately for the display and distraction phase of each trial, using generalized liner mixed models (GLMM; Baayen et al., 2008) with a Poisson error structure and logarithmic function (McCullagh & Nelder, 2019). In both models, display type (wait, invite, control), subject age group (infant, juvenile, adult), and species (orangutan, gorilla, chimpanzee, bonobo) were included as fixed factors. I scaled session number (1-6) to a mean of 0 and a standard deviation of 1 and included it as a fixed factor to assess and control for the effect of habituation across sessions. In the model examining the distraction phase, I included distraction type (clipboard, still face) as a fixed factor. I included subject ID as a random effect in both models. Unlike the study in Chapter 4, I included species as a fixed factor, given that it had fewer than five levels (Clark & Linzer, 2015). I calculated ratios of estimated mean rate of communication to assess the relative

effect size between each pair of levels of each predictor (R package emmeans, Lenth, 2019). I fitted the models and conducted the pairwise tests as in Chapter 4, using the same methods, R packages, and functions to derive *p*-values and prune random effect slopes and interaction terms. In each model, I ultimately omitted all random slopes within subject ID by these criteria. Similarly, I pruned all interactions between display type and each covariate fixed factor (age group, species, and session, respectively), and between distraction type and each covariate fixed factor (age group, species, and session, respectively), as none of these interactions were significant. I assessed multicollinearity as in Chapter 4, and there was no concern in either of the models (*GVIF*<2 for all factors, see **Appendix E**). All analysis was conducted in RStudio (version 4.2.1, RStudio Team, 2015).

Results

Display Phase

Subjects produced a mean (± SE) of 0.26 (± 0.01) communication behaviours per trial in the display phase. There was a significant effect of display type on communication behaviours in the display phase (χ^2=25.39, *df*=2, *p*<0.001). Pairwise tests showed that subjects communicated at a significantly higher rate in the "wait" condition than the "invite" condition (*z*=4.27, *df*=1, *p*<0.001, *ER*=1.43) and the control condition (*z*=4.31, *df*=1, *p*<0.001, *ER*=1.43). Subjects' rate of communication was not significantly different between the invite and control conditions (*z*=0.05, *df*=1, *p*=0.998, *ER*=1.008) (see Figure 5.2). An analysis of the ratios between estimated mean rates of communication (estimated ratio – *ER)* showed that subjects produced 43% more communication behaviours following the "wait" display than both the "invite" and control displays, while subjects produced only 0.8% more communication behaviours in the following the "invite" display compared to the control.
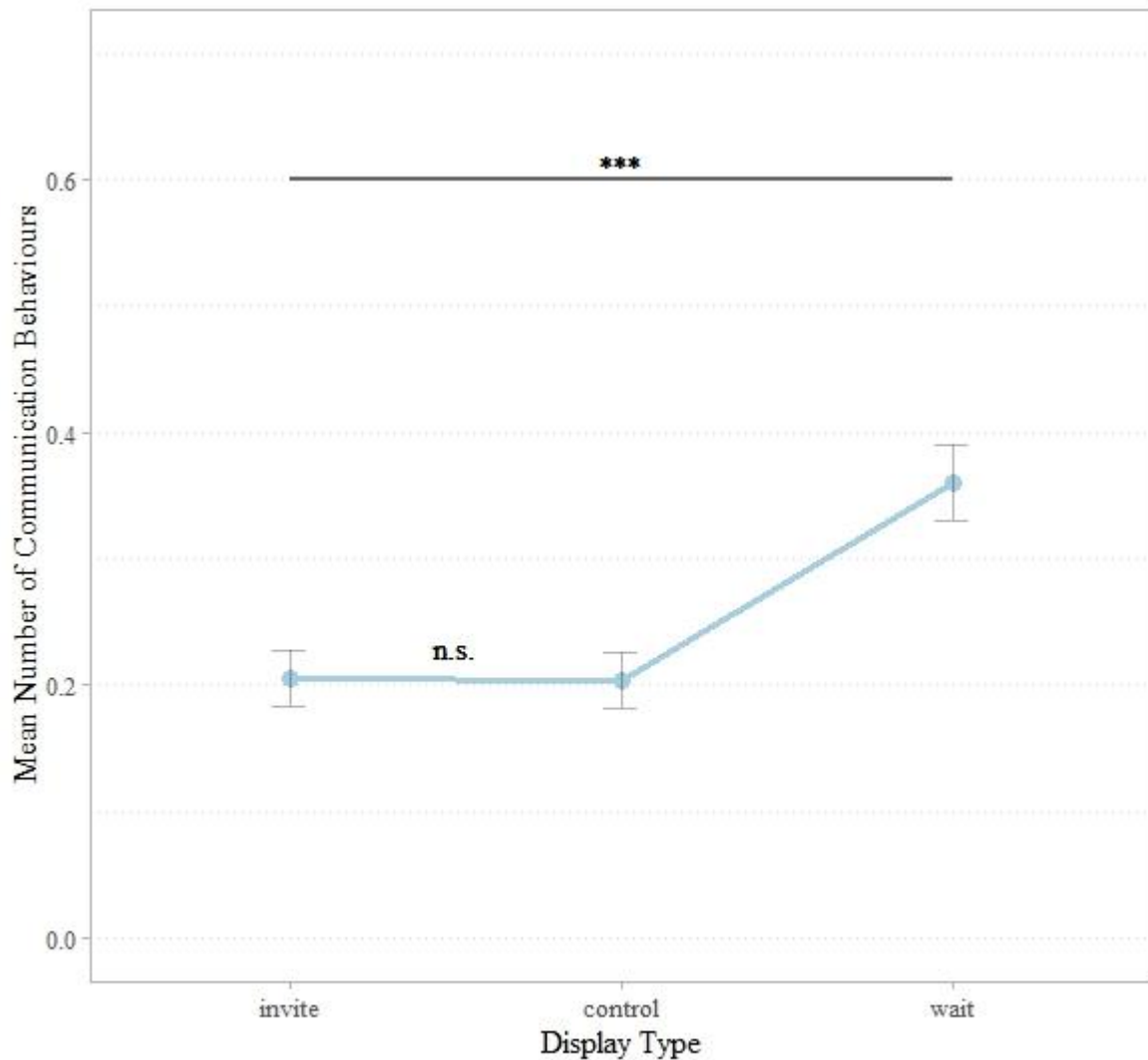
Figure 5.2 Mean number of communication behaviours in the display phase, separated by display type. The error bars represent standard error of the mean. ***p<0.001

Distraction Phase

Subjects produced a mean ($\pm$ SE) of 1.10 ($\pm$ 0.04) communication behaviours during the distraction phase of each trial. There was a significant effect of display type on communication behaviours in the distraction phase (χ^2=15.01, *df*=2, *p*<0.001). Pairwise tests showed that subjects communicated at a significantly higher rate following the "wait" display than the "invite" display (*z*=3.61, *df*=1, *p*<0.001, *ER*=1.21) and the control condition (*z*=3.01, *df*=1, *p*=0.007, *ER*=1.17). Subjects' rate of communication was not significantly different between the invite and control conditions (*z*=0.61, *df*=1, *p*=0.816, *ER*=1.04) (see Figure 5.3). An analysis of the ratios between estimated mean rates of communication (estimated ratio – *ER)* showed that subjects produced 21% more communication behaviours following the "wait" display than the "invite" display and 17% more behaviours than following the control display, and subjects produced 4% more communication behaviours in the following the control compared to the "invite" display.
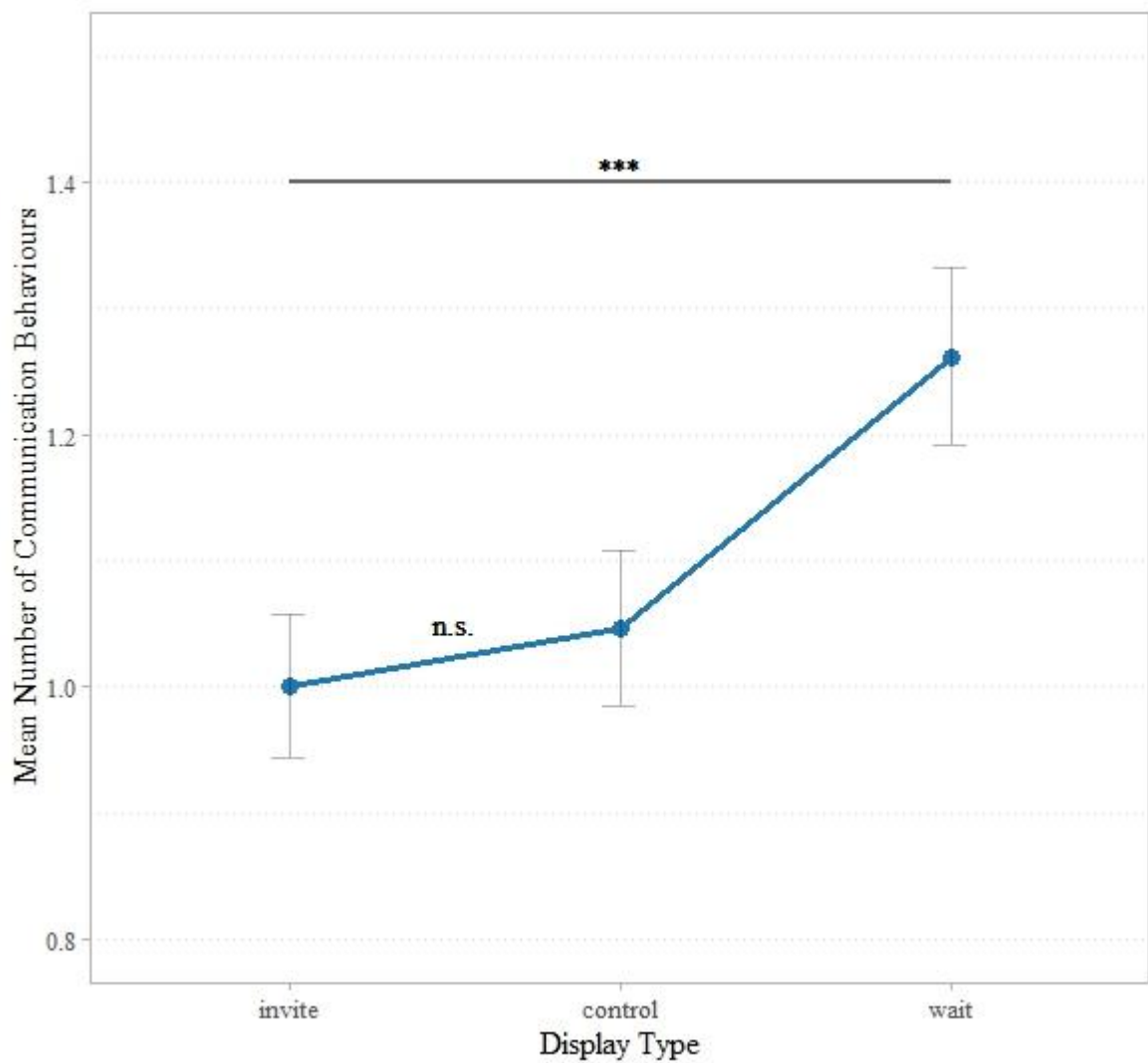
Figure 5.3 Mean number of communication behaviours in the distraction phase, separated by display type. The error bars represent standard error of the mean. ***p<0.001

Regarding the effect of distraction type, subjects produced significantly more communication behaviours in the still-face condition of the distraction phase, compared to the clipboard condition (χ^2=27.19, df=2, p<0.001, ER=1.32) (see Figure 5.4). Subjects produced 32% more communication behaviours in the still-face distraction condition than in the clipboard condition. There was no significant interaction between display type and distraction type on the pattern of communication behaviours.
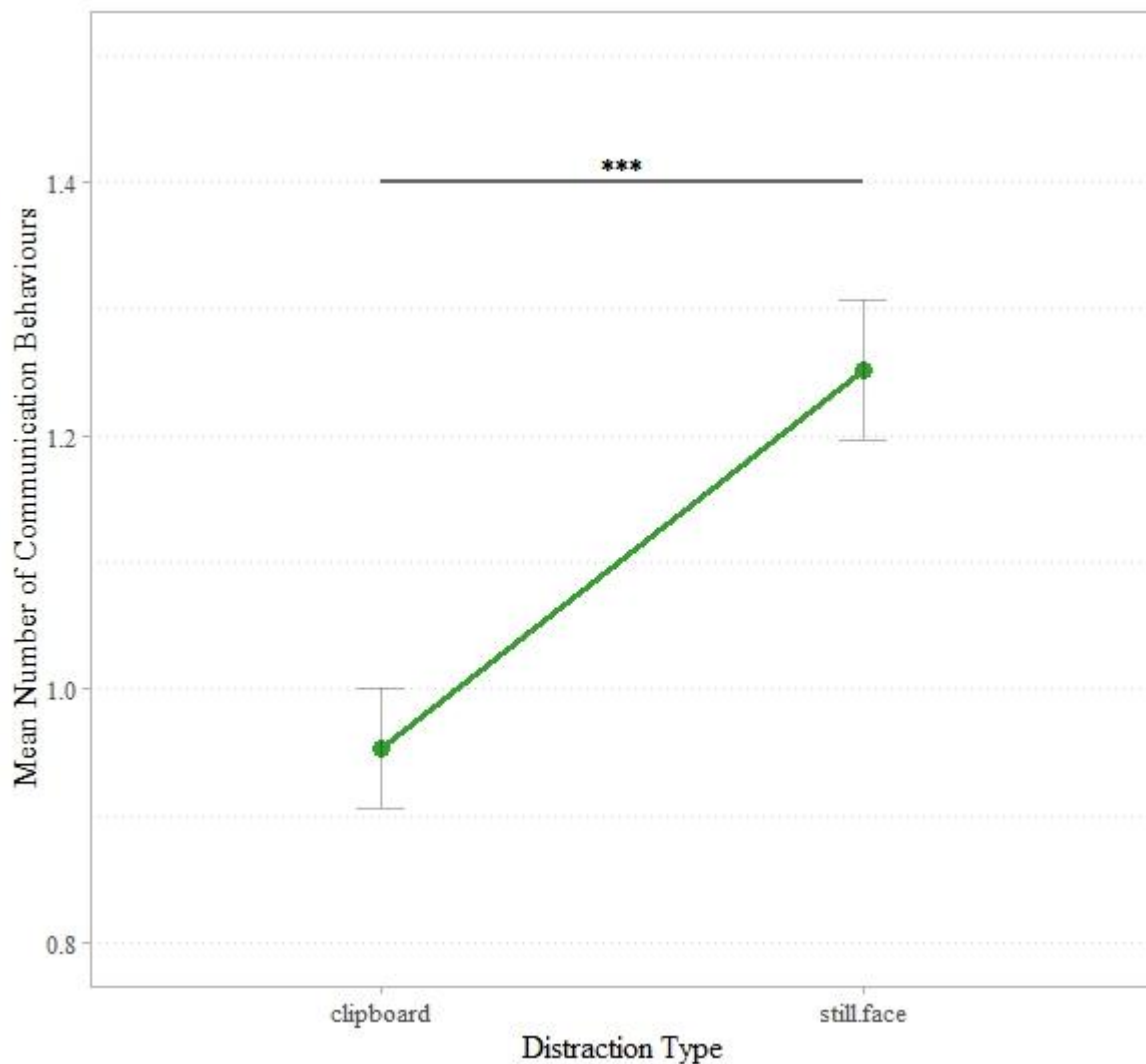
*Figure 5.4 Mean number of communication behaviours in the distraction phase, separated by distraction type. The error bars represent standard error of the mean. ***p<0.001*

Effects of Age

There was no significant effect of age group (χ^2=1.53, df=2, p=0.216) on the number of communication behaviours produced in the display phase. There was, however, a significant effect of age on rate of communication in the distraction phase (χ^2=5.37, df=2, p=0.021). Rate of communication in the distraction phase decreased with age; infants produced the most communication behaviours across all three display types, followed by juveniles, while adults produced the lowest rate of communication (see Figure 5.5Figure 5.6). There was no interaction of age with either display type or distraction type in either phase; the pattern of communication across display and distraction types did not differ significantly by age group.
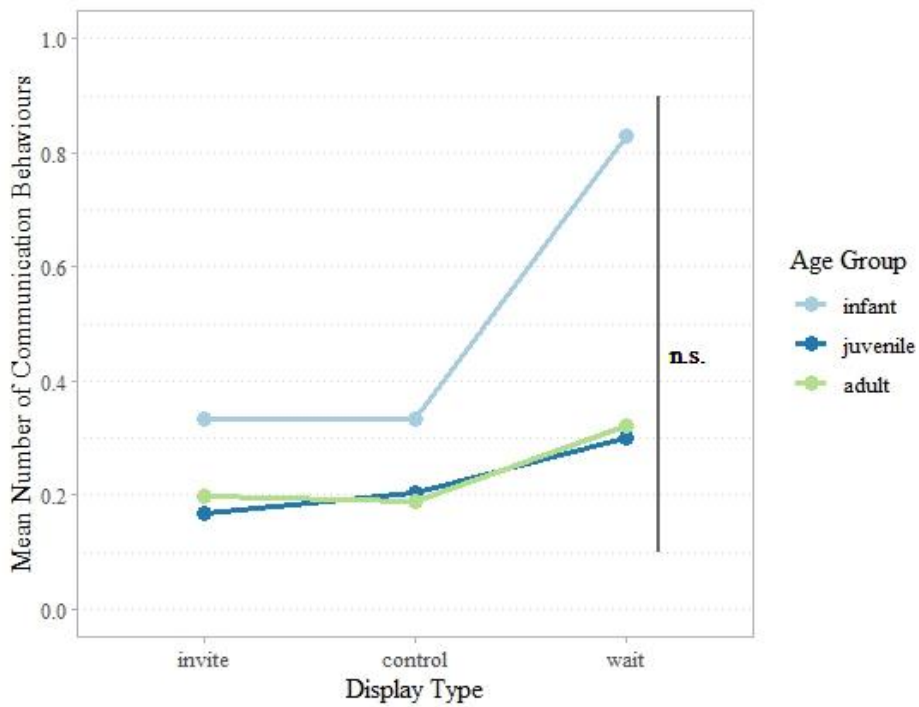
Figure 5.5 Mean number of communication behaviours in the display phase, separated by age group
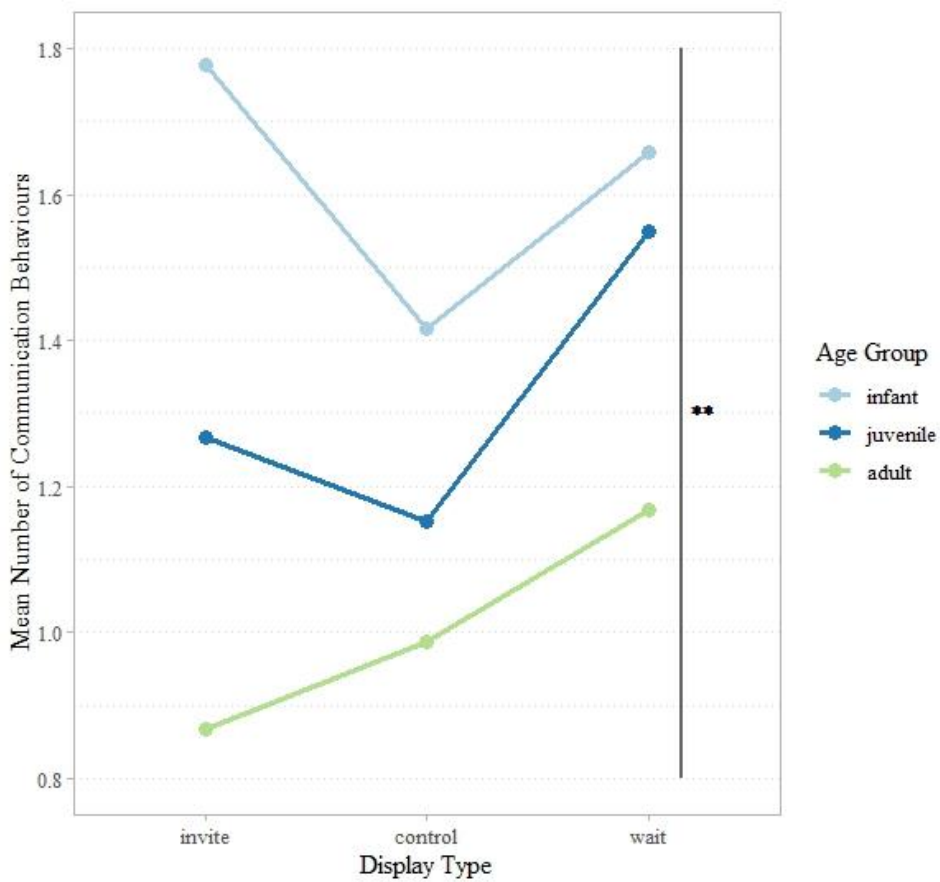
Figure 5.6 Mean number of communication behaviours in the distraction phase, separated by age group

Effect of Species

There was no significant effect of species (χ^2=1.35, *df*=3, *p*=0.718) on the number of communication behaviours produced in the display phase. There was a non-significant tendency toward an effect of species on communication behaviours in the distraction phase (χ^2=11.22, *df*=3, *p*=0.080); bonobos produced the most communication behaviours, followed by chimpanzees and orangutans. Gorillas produced the fewest communication behaviours in the distraction phase (see Figure 5.7 and Figure 5.8). There was no significant interaction of species with either display type or distraction type in either phase; the pattern of communication across display and distraction types did not vary significantly by species.
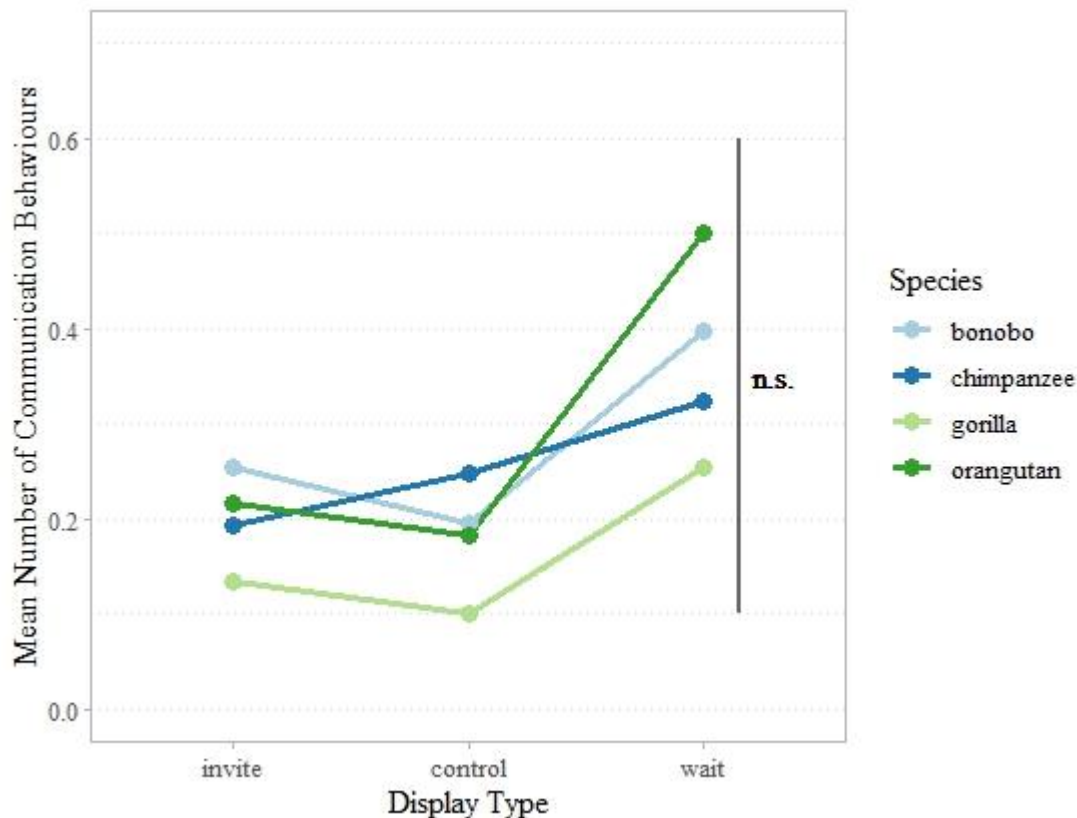
Figure 5.7 Mean number of communication behaviours in the display phase, separated by species
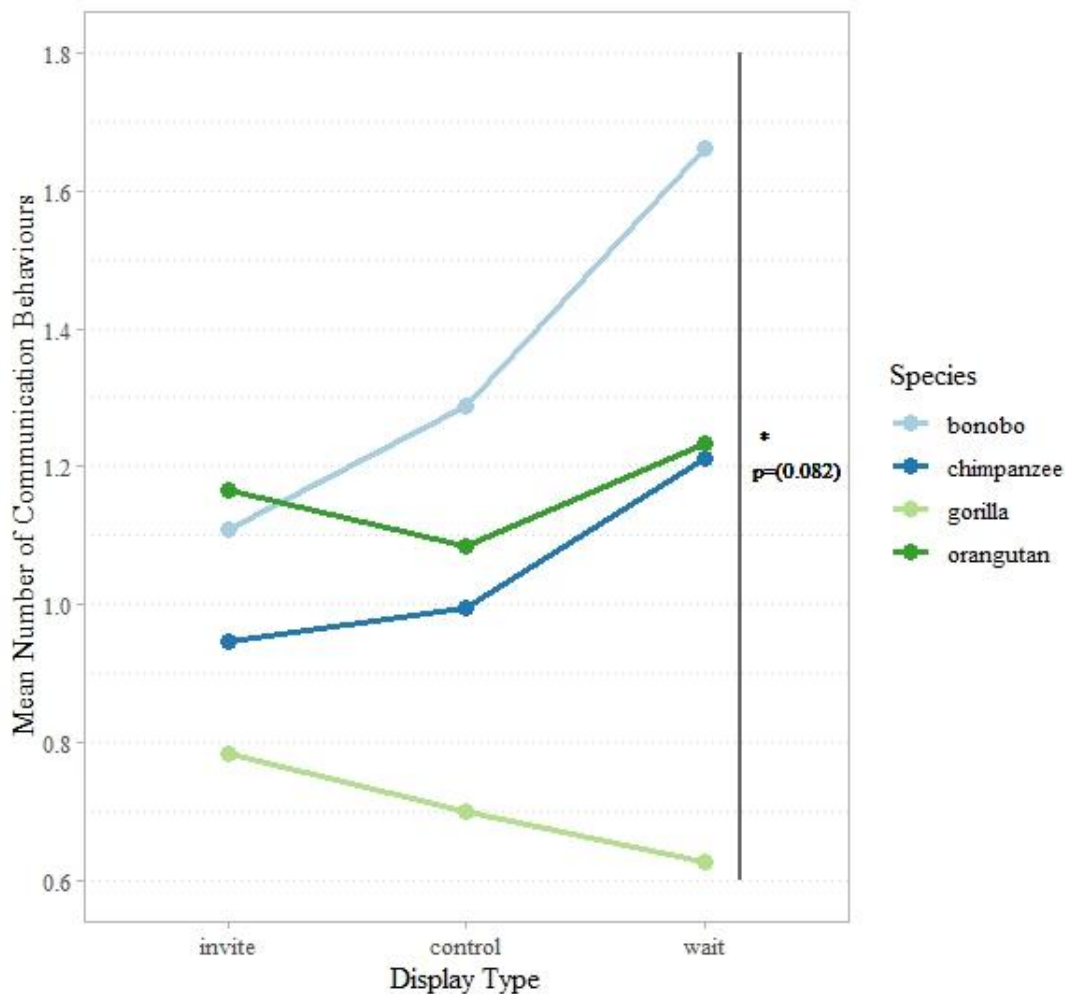
Figure 5.8 Mean number of communication behaviours in the distraction phase, separated by species

Effects of Session

There was no significant effect of session number (χ^2=2.60, *df*=1, *p*=0.107) on the number of communication behaviours produced in the display phase. In the distraction phase, the overall rate of communication behaviours did decrease significantly across the six sessions (χ^2=24.68, *df*=1, *p*<0.001). There was no significant interaction between session number and either display type or distraction type; subjects continued to show the increased rate of communication in the "wait" condition and in the still-face distraction type in later sessions (see Figure 5.9 and Figure 5.10).
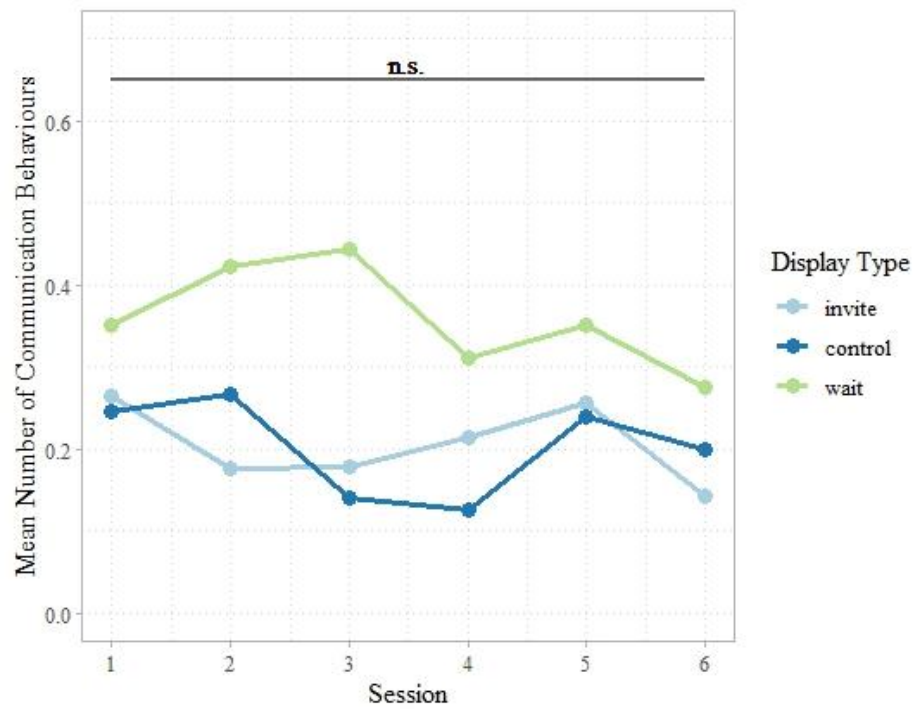
Figure 5.9 Mean number of communication behaviours in the display phase across sessions
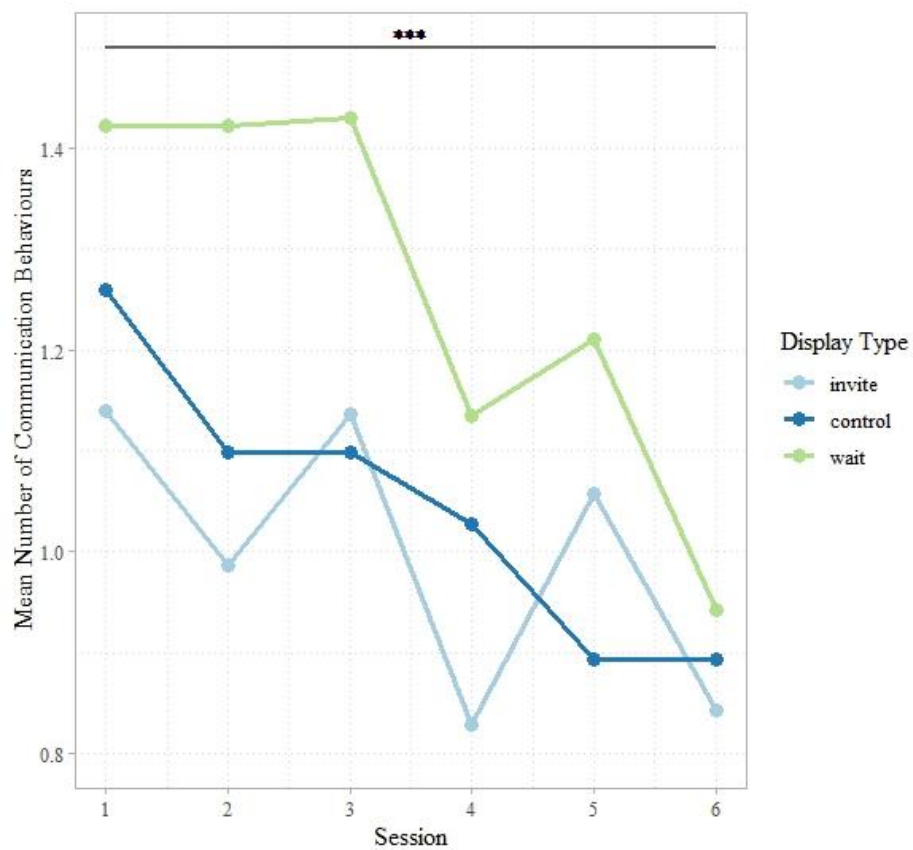
*Figure 5.10 Mean number of communication behaviours in the distraction phase across sessions, ***p<0.001*

Variation in Gesture Type

A descriptive analysis of variation in gesture type between subjects and between species revealed individual differences in gesture use; 27/36 subjects "preferred" a single gesture type (≥50% of individual's total gestures). Of the twelve behaviours recorded in analysis, five gestures were used more than 50% of the time by at least one subject (*finger thrust*: 11; *tap*: 8; *present mouth*: 5; *pass object*: 2; and *head nod*: 1). Within this sample of 27 subjects with a "preferred" gesture type, 26 subjects' second most-used gesture (≤35% of individual's total gestures) was also one of the above five gestures. There were species differences in the distribution of most-used gestures; bonobos were the only species to use *present mouth* ≥50% of the time, and gorillas were the only species to use *pass object* ≥50% of the time. Subjects in two species (chimpanzees and bonobos) used *finger thrust* ≥50% of the time, and *tap* was used ≥50% of the time by subjects in all four species (see **Appendix E** for individual gesture usage).

Table 5.3 Table depicting frequency of "preferred" gesture type (≥50% of individual's total gestures) separated by species.

Species	"Preferred" Behaviour (≥50% of total gestures)					
	finger thrust	tap	present mouth	pass object	head nod	none
Orangutan	0	3	0	0	0	2
Gorilla	0	2	0	2	0	1
Chimpanzee	8	2	0	0	1	5
Bonobo	1	3	5	0	0	1

Discussion

The results from this experiment support my hypothesis that apes are sensitive to the emotional valence of an experimenter's behavioural displays. Subjects showed a significantly higher rate of communication following the negatively valenced "wait" display than either the positively valenced "invite" display or the neutral and non-ostensive control. This suggests that the "wait" display alone increased subjects' motivation to express impatience from its baseline. This difference was present in both the display phase, as a direct reaction to the communication from the experimenter, and during the distraction phase, where increased communication behaviours are a proxy for decreased expectation that the experimenter will act. Given that both of the experimenter's behavioural displays were ostensive and involved the same attention-grabbing cues, it is unlikely that this effect is due to enhanced attention or sensitivity to ostension alone – the emotional valence of the display was key. The effect of emotional valence within ostensive communication has not, to my knowledge, been studied in non-human primates before, and the findings of the current study show that it may be a relevant driver of the effect of communicative displays.

There are two possible cognitive processes that could explain this change in rate of communication in response to displays with different emotional valences. The first is that the emotional valence of the display has bearing on the subject's interpretation of the meaning of the display – that is, their expectations about my subsequent behaviour were informed not only by the fact that communication occurred, but also by the emotional implication of the communication – I expressed a negatively valenced message (in the case of the "wait" display) and the subsequent interaction will therefore no longer facilitate the subject's desired outcome. While this interpretation comes closer to the subject interpreting semantic information from the message, compared to the paradigm in Chapter 4, it is still not necessary that the subject interpret an actual, specific message; they only need to process the emotional

context of the display and then relate it to similar past experiences with negatively valenced exchanges such as rejection or aggression. If the subject is indeed capable of the presumption of relevance associated with ostensive communication, they will apply the emotionally valenced context as relevant to their understanding of the communicative exchange and adjust their expectations for my subsequent actions. The alternative explanation for the effect of the negatively valenced display, however, is that the display induced a negative or impatient emotional state in the subject directly, not through the route of communication comprehension. By this account, the subjects increased their rate of communication following the "wait" display not because they understood the ostensively communicated context for the subsequent interaction, but because they had a learned or reflexive impatience response to negatively valenced behaviour, which resulted in increased protest behaviour. Although only the first explanation suggests that apes are engaging with ostension and incorporating the emotional valence of the display into their interpretation of the exchange, either explanation of this pattern of results demonstrates that emotional valence is a relevant quality of ostensive communication. Emotional valence influenced subjects' communicative responses and thus must be taken into consideration in paradigms investigating primates' behavioural reactions to ostension.

The effect of display type is not surprising, given existing empirical evidence that great apes can distinguish and match various emotions to their correct facial expression, using multi-modal cues (Parr, 2003). Whether apes used ostension to interpret the emotional valence of the displays or not, they distinguished between them, which is in line with the finding that primates are sensitive to variation in emotional expression. The current study is not able to distinguish between the two possible explanations for this pattern of results. A similar paradigm could separate the effects of an emotional state induced by the display and comprehension of the emotional context of the communication by introducing a control condition with a non-communicative, but emotionally valenced display, such as a picture of a conspecific ape with an aggressive facial expression (as in Kano et al., 2008). If the apes showed increased communication in the communicative, negatively valenced display, but not in the non-communicative condition, it would suggest that communication is the driver of this difference, and not merely the change in emotional state induced by the experimenter's tone or actions.

This experiment also showed that apes differentiated between the different distraction states of the experimenter, producing a higher rate of communication in the still-face condition than in the clipboard condition. As with the effect of emotional valence, there are two possible explanations for this pattern of results, reflecting two different levels of cognitive engagement with the production of communication behaviours. The first explanation is that subjects recognized that they did not have access to my visual attention during the clipboard display, and that their communicative behaviours were therefore not an effective means to reengage my cooperation. In this interpretation, the subjects were producing true intentional, goal-oriented communication – behaviours intended *for* the recipient, with the goal of reengaging or expressing protest following a lapse in cooperative behaviour. Sensitivity to the receptive (or otherwise) state of the recipient and voluntary production of communicative signals based on their attentional state would suggest that great apes are engaging in communication pragmatically, using the nature of the interaction – cooperative provision of food – to give context for their communication of protest or impatience. The alternative explanation, however, is again on the level of the emotional state of the subject. It is possible that subjects found the clipboard distraction less frustrating than the still-face display; perhaps they found the lapse in feeding more tolerable when I was occupied with a clear

alternative activity. This explanation is in line with unwilling/unable effects (Call et al., 2004), in which apes were more patient when the human experimenter was unable to provide the desired object, versus apparently able but unwilling. This explanation suggests that the "communication" behaviours are not necessarily *for* the recipient, that is, they are a reaction to the subject's own internal state of frustration and thus not necessarily communication. It is possible that subjects would express impatience regardless of my attentional state, as long as the source of my inaction was perceived as "unwilling" or spiteful, rather than a valid occupation. Although this interpretation does not necessarily support the argument that subjects engaged with the properties of communication (i.e., goal-orientation, attention) during these interactions, it does imply that they formed an interpretation of my motivations; their actions were informed by their differential understanding of why I was no longer feeding them. This is an example of social inference (see Chapter 3, section 4.1. Social Inference), which is an important building block of inferential and ostensive communication. Only one of the above explanations suggests that subjects communicated in a pragmatic manner in this experiment. Both explanations, however, find evidence that the behaviour of the other agent is a relevant factor in apes requesting and impatience behaviours – they are sensitive to the occupation of their communicative partner and their own rate of communication (or expression) is moderated by that understanding.

This design could be modified to differentiate between these two possible explanations for the sensitivity to distraction type. A future experiment could introduce an additional distraction state, in which the apes have access to the visual attention of the experimenter, but the experimenter is occupied by a clear task which prevents her from feeding the ape. For example, the experimenter could continue to face the subject with a neutral expression, as in the still-face distraction, but produce a scratching or grooming behaviour against her own body with both hands, thus temporarily preventing her from feeding the subject. Alternatively, or additionally, the design could include a distraction state in which the experimenter is not clearly occupied but is not facing the subject – staring into space in a different direction than the subject. Either or both of these distraction states would juxtapose access to the visual attention of the experimenter with the "validity" of cessation in feeding. If, for example, apes produced higher a higher rate of communication in the still-face distraction and the scratching/grooming distraction, but not in the clipboard distraction, it is more likely that their change in communication is about access to the experimenter's attention, and not their own internal frustration.

There was a significant effect of age group and a tendency toward an effect of species in the distraction phase of this experiment, which found that overall rates of communication varied between age groups and between species. The pattern of communication between display types and distraction types did not vary significantly by age group or species, suggesting that these effects were consistent across all groups, regardless of their mean or baseline rate of communication. There was no effect of age group or species in the display phase; groups communicated at similar rates in their initial reaction to the ostensive (or control) displays and varied only in their response once the experimenter became "distracted." These species and age differences followed expected patterns: infants communicated more than juveniles or adults, which is consistent with infants' developmentally immature capacity for patience and self-inhibition, and replicates the tendency of infant primates to be generally more interactive in social exchanges (Dutton, 2008). Species differences also generally followed an expected pattern: species whose wild counterparts live in larger and more complex social groups (chimpanzees and bonobos) communicated more than gorillas, who live in smaller groups with fewer social relationships (Yamagiwa et al., 2003, Gruber & Clay, 2016). Orangutans

communicated at a similar rate to chimpanzees and bonobos in this experiment, but this pattern may have been confounded by the fact that the sample of orangutans contained two of the three infants included in this study, and only five orangutans in total, elevating their overall rate of communication due to the effect of age. While these age and species effects do not change my interpretation of the results of this experiment in terms of ostension and emotional valence, they do show that the pattern of responses to the experimenter's behaviour persists regardless of the overall rate of communication within each group. It is also worth noting that although there was a significant effect of session number, wherein overall communication in the distraction phase decreased across the six sessions, the pattern of communication remained the same; subjects still communicated more in the "wait" display and still-face distraction conditions, even in later sessions. The fact that these effects persisted, even when the "invite" and control displays were equally associatively linked to a lapse in feeding, is evidence that subjects' responses were not the result of associatively learned reactions to the experimenter's behaviour, but due to their interpretation or immediate reaction to the behavioural displays.

Analysis of gesture type variation between individuals and between species revealed that individuals tended use the same gesture for over half of their total number of behaviours, and that the majority of these "preferred" gestures represented only four of the gestures included in my analysis. Each of these gestures (*tap*, *finger thrust*, *present mouth*, and *pass object*) are characterized as begging behaviours in existing captive ape literature (e.g., Call et al., 2004; Kaminski et al., 2004) and are deployed as measures of protest or impatience without differentiation between individual meanings of these gestures. These captive ape begging behaviours do not map seamlessly onto begging behaviours observed in wild apes (e.g., Gilby, 2006; Hobaiter & Byrne, 2014; Fröhlich et al., 2020), as wild ape begging gestures often involve direct tactile contact with the recipient or with the object of desire, which is often not possible in captive research settings. It may be impractical, therefore, to impose definitive, differential meanings onto these begging behaviours in order to analyse whether certain gestures might indicate referential, intentional communication while others are more likely to express impatience in the context of this study. Given that individuals appeared to favour a single gesture across all conditions, and that variation in gesture type occurred more at the level of species and subject than between individual trials, I suggest that analysis of gesture type between trials is not a practical method of parsing whether the behaviours in question were examples of referential communication or merely expressions of impatience. I do note, however, that this data is rich with potential for meta-analysis with other, similar studies, and could contribute to a more nuanced understanding of situational factors affecting gesture usage in captive apes.

A more fruitful line of inquiry into whether the behaviours measured in this study were indeed examples of referential communication is investigation of the manner in which the gestures were produced. Drawing from existing work on markers of intentional and referential communication in animals (e.g., Tomasello & Camaioni, 1997; Gómez, 2005), I suggest that these data could be further coded and analysed for behaviours such as attention-checking and response-waiting in conjunction with the production of begging gestures. If subjects were to produce gestures in combination with checking for the experimenter's attention or with waiting for a response before gesturing again, it would be more clear evidence that the subjects intend for the experimenter to see and react to the behaviours, which would indicate that they are intentional and communicative, rather than modulated by the subject's own internal state of impatience. Similarly, I propose investigation into whether any subjects produced their gestures in sequence, deviating from their most preferred gesture

after determining that it produced no reaction from the experimenter. There is some argument that gesture sequences do not *de facto* suggest that the communication is referential or goal-directed (Genty & Byrne, 2010; Tempelmann & Liebal, 2012). Sequencing in the context of this study, however, would suggest that subjects are not producing the behaviour stereotypically (at regular intervals regardless of the experimenter's actions) and may therefore be accounting for the context and the reaction of the experimenter in their production of begging behaviours (Graham, Furuichi, et al., 2020; Tanner & Perlman, 2017). If subjects were to differentially sequence their behaviours depending on the condition, it might suggest that they are doing so with a referential goal in mind, rather than displaying their own innate reaction to the frustration of waiting for the food reward. Evidence of referentiality and intentionality in these begging gestures could indicate that the apes are indeed producing communication behaviours, rather than only expressing impatience. This distinction could shed light on whether the behaviours are indeed *for* the experimenter, and thus, whether the effect of distraction type causes a difference in motivation to communicate.

Overall, the results of this study present evidence that any effect of ostensive communication on great apes' expectation of action from a human experimenter, may be moderated by the emotional valence of the communication. Whether this moderation occurs through the route of comprehension of the ostension and its emotional context or through modification of the emotional state of the subject, only the negatively-valenced ostensive display increased subjects' rates of communication from their baseline expression of frustration induced by a lapse in feeding. The results also show that the activity of the experimenter following the ostensive displays affected the rate communication behaviours, which is evidence that the ape subjects experienced the human as a relevant agent in the interaction, whose actions have bearing on whether the subject's goal to receive food will be met. As in Chapter 4, this study had the advantage of working with several relatively research-naïve subjects and with ape populations at two different sites, which smoothed out the effects of existing expectations for research interactions and specific husbandry practices that may have affected individual apes' patterns of behaviour. It also measured another natural, untrained response behaviour, which reduced the likelihood of an incidental response bias due to training. Also as in Chapter 4, subjects did not have to acquire an actual semantic message from the ostensive communication, which I believe reduces the confound of interspecific communication and permits a less human-cognition-oriented investigation of the capacity for ostension in primates.

This experimental design was not sufficient to detect whether the apes were truly communicating, or whether they were acting out of frustration in an independent manner, albeit influenced by the actions of the experimenter. To delve further into rate of communication as an appropriate behavioural response, it is vital to determine whether the communication behaviours are actually produced for the attention of the experimenter and whether they refer to a specific goal or reason for protest from the subject. Although a substantial body of research has shown that apes are capable of referential communication (e.g., Gómez, 2005; Slocombe & Zuberbühler, 2005; Pika, 2012), an experimental design using communication as a measure of comprehension should ideally be able to detect whether the communication produced in the testing situation is, indeed, referential. In such a design, communication behaviours from the subject could then be used to evaluate whether the subjects moderate their attempts to communicate based on the mental state of the experimenter (e.g., attentional state) or their past experience with the experimenter (i.e., common ground), which are both key components in the production of pragmatic and/or ostensive communication. To further explore the capacity for ostension in primates, and to

delve into their production of pragmatic communication, I next pursued an empirical paradigm that investigated the following question, using rate of communication as a response variable: will apes produce communication at different rates depending on contexts such as past experience with the recipient, or the recipient's ability to cooperate toward the subjects goal?

Chapter 6 Communication and Coordination in a Two-Action Task

Abstract

A vital element of context in pragmatic and ostensive communication is the common ground between the communicative partners – the shared experiences or shared knowledge upon which they may both draw to inform their communication to each other. Cooperative tasks place unique pressures on communication – agents must coordinate their actions toward a shared goal, which creates a rich foundation for common ground, especially the common ground of shared experiences. The purpose of this study was to investigate whether chimpanzees vary their production of communication based on the context of past experience of coordination with a human partner. Furthermore, this study investigated whether the communication that chimpanzees produced during the task was referential – soliciting help with the apparatus – or more generalized, requesting the food reward without reference to the necessary coordinated actions. In this experiment, ten chimpanzees learned to perform the second action in a cooperative, two-action task. Half of the subjects experienced the first action performed by me, a cooperative partner, and the other half experienced a non-social object performing the same function. Following a 100-trial learning phase to establish the fluid, successful, coordinated nature of the task, subjects were presented with two critical phases to probe their communicative efforts to solicit help from the human experimenter. First, a test phase, in which they had access to perform both actions on the apparatus themselves, and neither I nor the object performed the first action. Second, a follow-up communication phase, in which they could not perform the first action themselves, and I would, after a period of delay, perform the first action so that they could perform the second and receive the food reward. The results showed no effect of past experience of coordination in the learning phase. There were two effects of the perceived solvability of the apparatus on communication; subjects were more likely to communicate on trials where they did not subsequently correctly perform both actions and receive the food reward, and subjects were more likely to communicate after they had erroneously performed the second action in the absence of the first action, rendering the apparatus "impossible." These results do not clearly support the hypothesis that chimpanzees produce communication pragmatically in terms of past experience or task demands in a coordination setting. This pattern of results does fit in with existing literature suggesting that apes prefer to act on a task alone when possible, and only solicit help if there is no alternative action to take.[10]

Introduction

An important driver of pragmatic communication, especially ostensive communication, is the element of common ground – the shared knowledge or shared experiences from which the producer and the recipient can construct their message and make their interpretive inferences, respectively (Tomasello, 2009b; Reboul, 2010; Zuberbühler, 2017). Ostensive communication is generally understood to include the computation of the mental state of the

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other (Wilson & Sperber, 2002; Scott-Phillips, 2015; Moore, 2017; Heintz & Scott-Phillips, 2022), and a key component of mental state attribution is knowledge of whether information or experiences are mutually shared by both the producer and the recipient. In Chapter 3, I argue that both producers and recipients of communication can make inferences about others' goals or likely actions based on past experience, without necessarily needing to engage in ostension. The use of past experience to inform one's understanding of another's current or future actions is a form of social inference, which can be leveraged to facilitate flexible and pragmatic communication without rising to the level of ostension. In the present study, I probe chimpanzees' ability to moderate their communication on the basis of past experience, and thus engage in pragmatic communication, in the context of a coordination task.

The evolutionary relationship between cooperation and communication has been explored in depth in both humans and non-human primates. It has been suggested that the evolutionary pressure to cooperate may have driven the phylogenetic development of joint attention and shared intentionality and further facilitated the evolution of language in humans (Baldwin, 1995; Brinck & Gärdenfors, 2003; Tomasello, 2009b; Cheney & Seyfarth, 2012). Specifically, these authors posit that the prosocial nature of shared goals and the need to represent the motivations and actions of others led to the cognitive architecture necessary to engage with common ground. Communication and language follow as necessary means by which to coordinate actions and attention toward common goals (although see Reboul, 2010 for an alternative view of the evolution of shared intentionality). The intertwined connection between communication and cooperation is of interest in the study of non-human primate cognition, not only for the purposes of tracing the evolutionary roots of human communicative abilities, but also because primates engage in stable collective behaviours such as cooperative hunting in wild chimpanzees (Boesch, 1994, 2005), coordinated problem-solving in captive apes (e.g., Crawford, 1937; Chalmeau et al., 1997), and cooperative sharing of food or objects in both wild and captive apes (e.g., Hare et al., 2007; Yamamoto et al., 2009). Successful coordination and cooperation in non-human primates suggest that there are mechanisms of shared intention and flexible, goal-directed communication at play, but the extent of primates' flexibility and pragmatic application of communication in cooperative contexts is still not well understood.

There is substantial existing evidence that great apes are more successful at inferring others' intentions and motivations in competitive contexts than cooperative ones (e.g., Hare & Tomasello, 2004; Herrmann & Tomasello, 2006; Melis et al., 2006), although certain studies have found that communication does play a role in great apes' coordination of actions in cooperative tasks (see Duguid et al., 2020, for a recent review). Coordination tasks put pressure on the agents involved to represent at least their own actions, and, ideally, the actions of the other (Vesper et al., 2010), which creates the foundation for common ground based on past experience. Examining pragmatic communication in a coordination task allows a closer investigation of whether apes are engaging with common ground when they coordinate their actions with a partner. The present task examines chimpanzees' rate of impatience and requesting behaviours in coordination task with me, a human experimenter, as a measure of their efforts to solicit action from me. Unlike the studies presented in Chapter 4Chapter 5, this experiment does not ask whether the subjects are sensitive to human communication, but whether they are aware of and willing to solicit the actions of a human partner. As such, this task investigates not only pragmatic production of communication, but whether chimpanzees use their requesting behaviours to solicit an intangible resource – my actions – rather than the more commonly requested food or tools.

In the current study, I present chimpanzees with a task that requires two sequential actions to successfully deliver a food reward. This design is between-subjects; half of the chimpanzees learn the apparatus with me as a coordination task, and the other half experience the apparatus with an object performing my role. The first action, performed either by me or by a non-social object, manipulates the apparatus: I flip a small see-saw from one side to the other, causing a food reward to roll down its slope, where it lands on a piece of paper at the other end. The second action is always performed by the subject, who pulls the strip of paper toward themself, out of the apparatus, bringing the food reward with it. These actions are dependent on one another; pulling the paper before flipping the see-saw will result in a failure to retrieve the reward. Thus, the apparatus is rendered "impossible" if the subject pulls the paper too early, and my ability or willingness to flip the see-saw is made irrelevant in that instance. Subjects experience their learning condition – human or object – over a long period of exposure, with no need to communication to facilitate the coordination. I flip the see-saw (or allow the object to act on the see-saw) immediately after it is baited, until the subjects are accustomed to the fluid and successful procedure of the task. Once the nature of the task is established with each subject, I probe for communication in two different critical phases. First, a test phase, in which the subject has access to flip the see-saw themselves, if they innovate this solution, or to communicate in attempt to solicit my help with the apparatus. In the test phase, I do not ever perform the flipping action to help the subject. In the second critical phase, however, the subjects do not have access to flip the see-saw themselves; the only action they can take toward successfully retrieving the reward is to communicate to solicit my help. In this follow-up phase, I do help the subject, after a period of delay during which they may attempt to solicit my help.

The purpose of this study is to examine whether chimpanzees vary their production of impatience and requesting behaviours pragmatically based on the context of shared past experience with a coordination partner. Common ground, where shared past experiences create mutually-held knowledge, is a key element of ostensive communication – it is the basis on which relevant inferences are made to interpret meaning. If apes are capable of moderating their communication based on past experience, it would constitute an important building block toward assessing whether apes also moderate their communication based on shared knowledge. Differential production of communication based on past experience in the current paradigm would rise to the level of pragmatic communication; the subjects would be accounting for their own past experience with me. This design cannot detect whether they are also accounting for my awareness of our mutual past experience, which would constitute ostensive communication – they may simply presume that I will continue to act as I have done, without further computing my interpretation of the task in the moment. This study also examines whether chimpanzees vary their rate of communication situationally depending on their own ability to successfully manipulate the apparatus. If subjects communicate more frequently when the apparatus is still possible to solve (i.e., if they have not yet rendered the apparatus impossible by performing their own action out of order) it would suggest that their communication is about the apparatus, and not just a request for the food reward. This pattern would elaborate on existing findings that apes are capable of producing imperative requests not only for food directly, but for objects that will allow them to acquire food, such as hidden tools (Call & Tomasello, 1994; Zimmermann et al., 2009). Here, subjects would be requesting neither food nor an object, but instead an action that facilitates their receipt of food. Such a finding would be evidence of inferential communication (see Chapter 3), in that the subject is accounting for their knowledge of my competency in the task and producing ambiguous gestures from which I may infer that they are requesting the flipping action, based on the task at hand.

The predictions for this study are as follows: first, if subjects moderate their production of impatience and requesting behaviours based on their past experience of coordination, I expect that subjects in the human learning condition will communicate to engage my help more frequently than those in the object learning condition, who have no experience with my help during the task. Second, I predict that, if subjects are communicating referentially, and requesting help about the apparatus specifically, both groups should communicate more frequently when I can still act successfully on the apparatus (i.e., when the apparatus is still baited with a strip of paper). Conversely, if subjects' communication represents more general requesting and begging for the food reward, and not a request for action on the apparatus, it should not vary by the state of the apparatus (possible or impossible).

Methods

Subjects

Subjects for this study included 10 chimpanzees (*Pan troglodytes*), housed at RZSS Edinburgh Zoo. The subject group included 1 juvenile (aged 5 years) and 9 adults (aged 21-46 years). The subjects' enclosure included access to both indoor and outdoor areas, with food, water, and enrichment available ad libitum. Subjects varied in rearing history and are classified as follows: *wild* (subject born and reared throughout infancy in a wild environment) or *parent* (subject was reared in captivity by parent and other conspecific individuals, or parent-reared with minimal assistance from human caregivers). All subjects in this experiment had past experience with interactive cognitive research with a human experimenter, including tasks requiring manual manipulation of an apparatus to retrieve food, but no subjects had experience with the exact apparatus or task used in this protocol. This experiment was between-subjects, and subjects were assigned to experimental conditions in a pseudo-randomized, counterbalanced manner, to ensure equal distribution of sex. **See Table 6.1 for detailed subject demographics. [11]**

Table 6.1 Subject demographic information and experimental condition assignment

Name	Age	Sex	Rearing History	Experimental Condition
Lucy	43	F	Parent	Human
Eva	39	F	Parent	Human
Kilimi	27	F	Parent	Object
Edith	24	F	Parent	Object
David	46	M	Parent	Object
Louis	44	M	Wild	Object
Qafzeh	29	M	Parent	Human
Frek	26	M	Parent	Human
Liberius	21	M	Parent	Object
Velu	5	M	Parent	Human

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Materials

I conducted testing for all individuals and was familiar to all individuals prior to the start of this experiment. I tested the subjects individually, but subjects were not separated from groupmates for testing, and it was therefore possible for other individuals to observe or

interfere with testing. As this experiment was between-subjects, I did not administer any trials or interact with the apparatus if any subject in the opposite group from the testing individual was in the research room. If a subject from the opposite group entered the research room during testing, I halted and restarted the trial once they left, so that subjects were not able to observe the other group's learning condition. During the test and communication phases (see below), I did not proceed with trials if any other individual, regardless of experimental group, was in the research room, unless they were not participating in or had already finished the full study. Regardless of phase, I did not proceed with trials until the testing individual was not interacting with or distracted by any conspecifics, and I halted and restarted trials if interrupted by a conspecific, even if the conspecific was in the same experimental group.

I conducted testing in the research rooms of the BRU (see **Appendix B**). The apparatus for this study consisted of a small wooden see-saw constructed with a ridge along one side (to prevent food rewards from rolling off) and a shallow groove on the other side, which was baited with a strip of paper. The see-saw functioned such that if a food reward was placed on the ridged side with the ridged side slanted down, I could use my hand to flip the see-saw toward the grooved side, and the food reward would roll into the groove, where the subject could retrieve the food by pulling the strip of paper toward themselves (see Figure 6.1). The apparatus also included a weighted lever (constructed of a 20cm piece of wood with a weight attached near the top) affixed to a long piece of string. The lever rested on the table in front of me, next to the grooved side of the see-saw, and I held the piece of string tightly under the table, out of view of the subject. The lever functioned such that, if I released the string, it would fall and hit the grooved side of the see-saw, flipping it toward that side, without the appearance that I had directly manipulated the apparatus (see Figure 6.2).
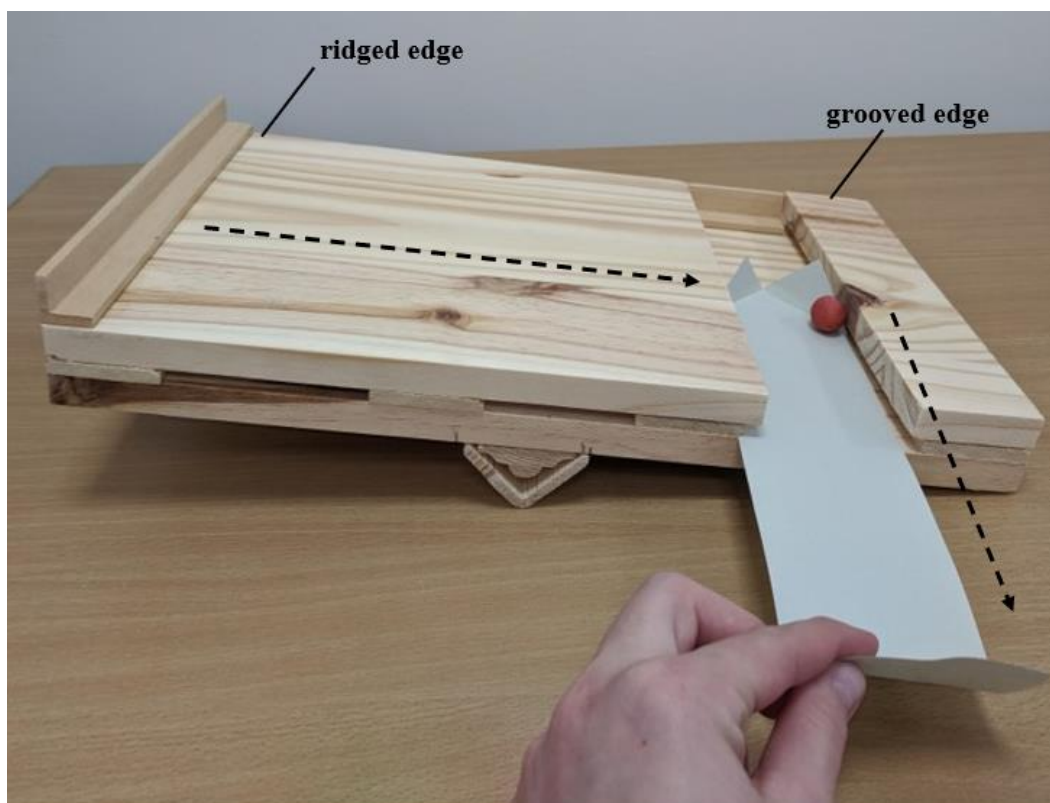
Figure 6.1 Depiction of the see-saw apparatus flipped toward the grooved edge. Dashed lines indicate the path of the food reward as it rolls from the ridged edge to the grooved edge and is pulled toward the subject using the paper.

I placed the apparatus on a table secured into an alcove in the human area in the BRU, surrounded by windows with mesh or polycarbonate panels to the subject's area on three sides (see Figure 6.2, see also panel 7, panel 8, and panel 9, in the BRU, **Appendix B**). These panels were arranged such that subjects could access the apparatus on the table by sticking their fingers through the mesh from the side (at panel 7, during certain phases) or by pulling the paper from the front (at panel 8, during all phases). Panel 9 was always blocked by transparent polycarbonate; it was not possible for subjects to access the seesaw from that side. I positioned the see-saw such that subjects could reach the grooved edge, but not the food reward, by pushing their fingers through the mesh at panel 7, and such that subjects could reach the paper, but not the see-saw itself, through the mesh at panel 8 (see Figure 6.2). The table included a sliding platform, which allowed me to move the entire apparatus back and forth for baiting and presentation during trials.
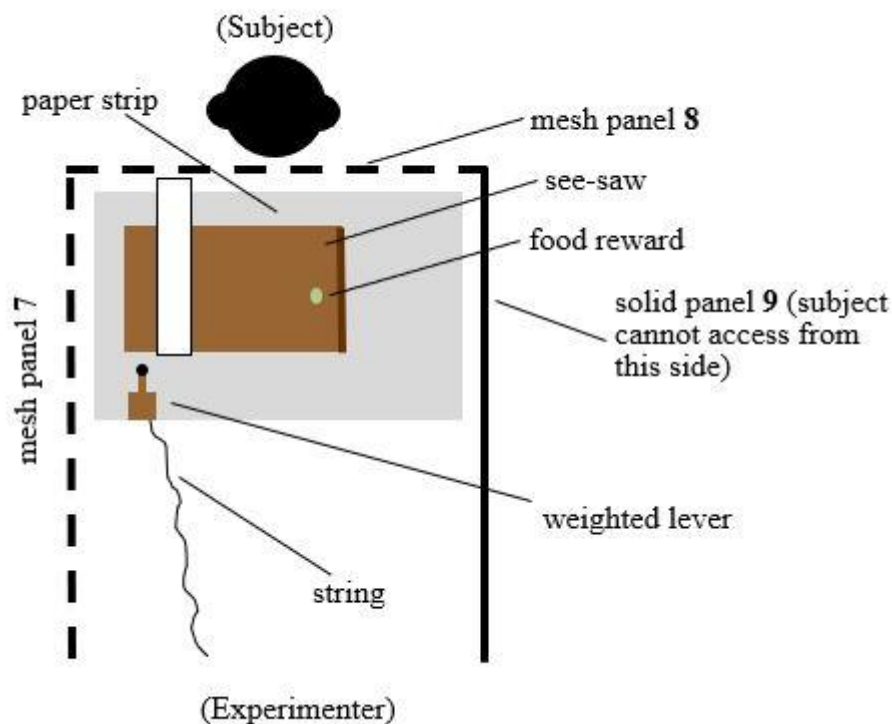
Figure 6.2 Bird's eye view of the see-saw apparatus and testing set-up.

I baited the apparatus with a high-value food reward (a whole grape, to facilitate rolling). I used a cardboard occluder to obscure the see-saw from view during baiting, so that subjects could not see me use my hands to orient the see-saw with the ridged side down at the start of each trial. In accordance with safety protocols related to COVID-19, I wore a mask and clear face shield during testing, which obscured my nose, mouth, and chin, but did not prevent subjects from observing the position of my head, eyes, body, or hands. All trials were videotaped using two cameras: one from my perspective, looking directly forward at panel 8, and one positioned at panel 9, to capture activity occurring in front of panel 7.

Procedure

The experiment consisted of four phases: a pre-training and habituation phase, a learning phase, a test phase, and a communication phase. The design was between-subjects; the protocol was identical between groups during the pre-training, test, and communication phases, but different during the learning phase. Subjects were divided into two groups – those who learned the apparatus in coordination with me, the human experimenter ("human") and those who learned the apparatus with an inanimate object ("object").

Pre-Training and Habituation Phase:

The pre-training and habituation phase consisted of three protocols to ensure that subjects were familiar and comfortable with the properties of the apparatus, and to establish that subjects could meet the minimum task demands to successfully operate the apparatus.

Paper Habituation

This protocol served two purposes: first, subjects demonstrated that they intuitively understood to pull a piece of paper through the mesh to access a food reward, and second, subjects had the opportunity to experience the outcome of pulling a baited piece of paper versus an empty one. I placed two strips of paper with either a 10 cm or a 30cm gap between them, such that the subject could reach and pull the end of either strip of paper through panel 8 (I delivered close and far trials in one block of six trials each, with the order of distance counterbalanced by subject). Panel 7 was blocked by a polycarbonate panel; subjects could not access the table from that side. I then placed a half-grape on top of one strip of paper and on the table next to the second strip (I counterbalanced the baited location in a pseudorandomized order, with no more than three trials in a row to the same side). I allowed subjects to pull the first strip of paper that they touched through the mesh and removed the other strip and food reward. If the subject chose the baited strip of paper, they were able to access the food reward. I administered 12 trials of this protocol per subject and then moved them to the next pre-training stage no matter what their pattern of choices – this stage was intended for habituation only. Of the fifteen chimpanzees at Edinburgh Zoo, ten intuitively pulled the paper through the mesh with no training. Five chimpanzees did not show interest in the paper strips and were not included in the final sample.

Inhibition Training and Pre-Test

The second stage of pre-training was intended to train subjects to wait to pull the paper until it was baited with a food reward. I placed a single strip of paper such that the subject could reach and pull it through the mesh at panel 8 at any point. Panel 7 was blocked by a polycarbonate panel; subjects could not access the table from that side. After 0, 3, or 5 seconds, I placed a half-grape on the piece of paper (I counterbalanced the order of times across twelve-trial sessions in a pseudo-randomized order, with no more than three trials in a row with the same time delay and no 12-trial session beginning with a 5-second trial). Subjects were required to inhibit their desire to pull the paper until it was baited with the grape. I advanced subjects to the next pre-training stage according to the following protocol: all subjects received one 12-trial session to habituate them to this task. Following that, subjects received blocks of two 12-trial sessions until they reached a passage criterion of waiting to pull on 13/16 critical trials (0-second trials were omitted from this metric) across

those two blocks. All ten subjects who participated in the paper habituation stage passed this criterion after a maximum of 11 blocks of two 12-trial sessions (see **Appendix F** for details).

Apparatus Habituation

To habituate subjects to the see-saw apparatus, and to ensure that their inhibition to pull the paper until it was baited with a grape transferred to the see-saw itself, I administered 24 preliminary trials with the apparatus to each subject. This apparatus habituation was conducted with the subject seated at panel 8. Panel 7 was blocked by a polycarbonate panel; subjects could not access the table from that side. I oriented the see-saw such that it was already in the "down" (flipped toward the groove side) position. I prepared the apparatus behind the occluder, and the subjects could not observe the flipping motion of the see-saw during this pre-training. I then removed the occluder, slid the table forward, such that the subject could reach the paper strip, and placed a grape on the ridged side of the occluder. Thus, subjects had the opportunity to observe the grape roll down the see-saw and land in the groove on the paper strip, where they could then pull the paper to access the food.

Learning Phase

This phase constituted the between-subjects aspect of the experimental protocol. I conducted learning trials with the subject seated in front of panel 8. Panel 7 was blocked by a polycarbonate panel; subjects could not access the table from that side. In both conditions, I oriented the see-saw toward the ridged side and baited the groove with a piece of paper, before placing a whole grape on the ridged side. This manipulation always occurred behind the occluder, so subjects could not observe my actions. Then either:

Human Condition (Coordination): I pushed the table forward until the paper strip was within reach of the subject and removed the occluder, continuing to face toward the chimpanzee at panel 8. Immediately, I used my hand to flip the see-saw toward the grooved side. During this manipulation, I continued to hold the string of the weighted lever tightly, out of view of the subject, so that the lever did not descend onto the see-saw. The grape then rolled down the see-saw, into the groove, and the subject was able to retrieve it by pulling the piece of paper.

Object Condition (Non-Coordination): I pushed the table forward until the paper strip was within reach of the subject and removed the occluder, simultaneously turning my head and body to the right, toward panel 9 and away from the table, subject, and apparatus. While looking away, and out of view of the subject, I released the string of the weighted lever, such that it fell on the see-saw and caused it to flip toward the grooved side. The grape then rolled down the see-saw, into the groove, and the subject was able to retrieve it by pulling the piece of paper.

In both conditions, I allowed the subject to retrieve the grape, then pulled the sliding table backward, replaced the occluder, and baited for the next trial. Subjects received 100 learning trials, delivered in 10-trial sessions.

Test Phase

In this phase, subjects had the opportunity to operate the see-saw themselves. This phase was intended to probe subject's understanding of how to operate the see-saw, following their learning condition. This phase also examined whether the subjects produced any communicative behaviours toward me, in efforts to reengage or recruit my help with the apparatus. I initiated trials with the subject sitting at panel 8, but panel 7 was no longer blocked by polycarbonate; subjects could access the grooved end of the see-saw through the mesh on that side. I baited the apparatus with paper and a grape as in the learning phase, and then pushed the table forward and removed the occluder. As in the learning phase, the weighted lever was present, but was secured to the table, so it would not fall and flip the see-saw. I then sat, with neutral posture and facial expression, facing the subject, and did not move to flip or interact with the apparatus. Subjects were permitted to interact with the apparatus freely for 60 seconds – they had the opportunity to move around to panel 7 and flip the see-saw themselves before pulling the paper. Subjects were also able to pull the paper out of the see-saw without flipping it and were able to flip the see-saw by other means (e.g., using a stick, using the paper as a lever, etc.). If subjects pulled the paper before flipping the see-saw (rendering the state of the apparatus "impossible" – they could no longer retrieve the grape even if the see-saw were later flipped), I terminated the trial after 30 seconds from the time that they pulled, or 60 seconds from the beginning of the trial, whichever came first. If the subject did not pull the paper, the trial lasted for 60 seconds. If the subject flipped the see-saw, the trial ended immediately, I permitted the subject time to retrieve the grape before resetting the apparatus. Each subject therefore had a minimum of 30 seconds to observe and interact with the apparatus on each trial if they did not correctly operate the see-saw and retrieve the reward. I administered one 12-trial session per subject in this phase, for a total of 12 test trials.

Learning Condition Refresh Phase

In order to refresh all subjects' memory of their original learning condition, I administered a block of 10 trials using the same procedure as the original learning condition for each subject, following their competition of the test phase.

Communication Phase

This phase was intended to probe subjects' willingness or likelihood to produce communication behaviours toward me when I was no longer performing my role (for those who experienced the "human" learning condition) or when the apparatus was not functioning as expected (for those who experienced the "object" learning condition), and when the subjects are unable to operate the apparatus themselves. Trials proceeded as in the test phase – I baited the apparatus and presented it to the subject, and I did not move to operate it, but panel 7 was blocked once again, so subjects were unable to operate the see-saw themselves, even if they had innovated this solution in the test phase. After a period of 10, 20, or 30 seconds (counterbalanced and presented in a pseudo-randomized order with no more than three of the same time-delay in a row), I used my hand to flip the see-saw and the subject was able to use the paper to retrieve the grape, if they had not already pulled it out of the apparatus. I then slid the table backward and baited the apparatus for the next trial behind the occluder. I was not responsive to any communicative behaviours from subjects – I maintained a neutral expression and position until the designated time to flip the see-saw. In the event that the subject successfully flipped the see-saw or retrieved the grape by alternative means

(e.g., using a stick), I repeated the trial. I administered two 12-trial sessions per subject in this phase, for a total of 24 communication trials each.

Scoring and Analyses

I scored subjects' actions toward the apparatus and communication behaviours toward me from video recordings for both the test and communication phases. With regard to action, I scored subjects' flips of the see-saw as a binary variable (0 = no correct flip, 1 = correct flip by any means). This variable served as a proxy for correct trials; trials in which the subject first pulled the paper and then flipped the see-saw (correct manipulation of the see-saw, but in the wrong order, and thus failure to successfully use the see-saw to acquire the food reward) were counted as "0" (no correct flip). I further categorized flipping into an additional binary variable (0 = flip by any alternative means such as using the paper as a lever, 1 = "proper" flip by pressing the hand against the grooved side of the see-saw), for some analyses, to assess group differences in flip style. I scored subjects' "incorrect" pulling of the paper as a binary variable (0 = no pull or pull occurring after the see-saw is flipped, 1 = pull occurring before the see-saw is flipped). I used the pull response compute a pre-pull and post-pull state of the apparatus in each trial for both the test and communication phases. I could therefore categorize communication behaviours in either phase as "pre" or "post" pull according to their timing in the trial relative to the subject pulling the paper. On trials in which the subject did not pull at all, or pulled "correctly" (pulling after either they themselves, or I, the experimenter, flipped the see-saw), the pre-pull state lasted the entire length of the trial.

Communication behaviours included a mixture of acts commonly used by captive chimpanzees to request food or express protest toward humans (see Table 6.2) and were included if they were performed within one arm's reach of the mesh panel. I counted repetitive acts (e.g., nodding, tapping) only once per bout, unless the act fully ceased for at least 1 second before beginning again, or the subject changed the location of the behaviour within the mesh panel. I collapsed communication behaviours by type for each subject and coded them as the total count of communication behaviours per trial. For certain analyses, I split communication behaviours into a count of "pre-pull" and a count of "post-pull" behaviours per trial. I conducted behavioural coding using BORIS, an open-source event-logging software (Friard & Gamba, 2016).

*Table 6.2 Ethogram of communication behaviours. See **Appendix F** for more detailed criteria for coding these behaviours.*

Behaviour	Definition
tap	the subject taps or raps their fingers or hand against the table, mesh, or feeding tube
finger thrust	the subject thrusts their fingers (or single finger) through the mesh
present mouth	the subject presents their lips or mouth, open or closed, through the mesh
head nod	the subject moves their head up and down rapidly and repeatedly (at least two movements)
hand fling	the subject raises their hand upward and produces a flinging gesture toward the shoulder
pass paper	the subject pushes or holds strips of paper, available from earlier trials, through the mesh
grumble	the subject produces an audible, low-pitched vocalization, akin to a grunt, grumble, or cough
whine	the subject produces a high-pitched vocalization akin to a whine or cry
raspberry	the subject produces a lip buzzing/raspberry sound

An additional coder, naïve to the empirical questions and predictions of this study, scored communication behaviours for 15% of trials. I assessed interobserver reliability using Cohen's kappa for the occurrence of action behaviours and intraclass correlation coefficient for the total number of communication behaviours per trial. I calculated ICC using a two-way, absolute-agreement, random-effects model with a 95% confidence interval. Interobserver reliability was very good across all response variables (test phase, flipping (any): $K=1$, $N=18$, $p<0.001$; test phase, flipping (type): $K=1$, $N=18$, $p<0.001$; test phase, pulling: $K=1$, $N=18$, $p<0.001$; test phase, communication: $ICC=0.854$, $CI=0.657\text{-}0.942$; communication phase, pulling: $K=1$, $N=36$, $p=<0.001$ communication phase, communication: $ICC=0.832$, $CI=0.648\text{-}0.918$).

I analysed the effect of learning condition (human, object) on both action and communication behaviours using generalized liner mixed models (GLMM; Baayen et al., 2008). For flipping behaviour in the test phase, I conducted the analysis using two GLMMs with a binomial error structure and a logit link function: one to examine the overall frequency of correct flips across all test trials, and one to compare flip style between groups only on trials with a flip. For communication behaviour in both phases, I conducted the analysis using two GLMMs with a Poisson error structure and logarithmic function (McCullagh & Nelder, 2019). In all models, I included condition (human, object) as a fixed factor. I scaled trial number to a mean of 0 and a standard deviation of 1 and included it as a fixed factor in all models to assess and control for the effect of learning across sessions (I excluded trial number from the model comparing flip style between groups, as this analysis included only certain trials per subject). In models examining frequency of communication, I included the state of the apparatus (pre-pull, post-pull) as an additional fixed factor. In these models, I also included the duration of the trial and the duration of the pre-pull period as fixed factors to control for the differences in amount of time available in which to produce communication behaviours. I included subject ID was included as a random effect in all models, apart from the model examining flip style, as flip style had zero variance within subjects – all subjects used one or the other flip style exclusively. I fitted the models and conducted the pairwise tests as in Chapter 4, using the same methods, R packages, and functions to derive *p*-values and prune random effect slopes and interaction terms. In each model, I ultimately omitted all random slopes within subject ID by these criteria, except in the model comparing flipping success in the test phase, where I included trial number as a random slope within subject ID, to control for the effect of change in flipping over trials on an individual basis. I conducted pairwise comparisons between the two conditions (human and object) and between the pre- and post-pull state of the apparatus for certain models, including odds ratios (for binomial models) and

ratios of the estimated rate (for the Poisson models) to assess the relative effect size between each pair of levels of each predictor (R package emmeans, Lenth, 2019). I assessed multicollinearity as in Chapter 4, and there was no concern in either of the models (*GVIF<2* for all factors, see **Appendix F**). All analysis was conducted in RStudio (version 4.2.1, RStudio Team, 2015).

Results

Action-Learning

In the test phase, six of the ten subjects flipped the see-saw on at least one trial. Of those six subjects, two subjects used the "proper" method of flipping, wherein they used their hand to move the grooved edge of the see-saw downward. The remaining four subjects flipped the see-saw by alternative means, such as using the paper as a lever to manipulate the see-saw. There was no crossover between flipping methods; subjects who flipped the see-saw used exclusively one method or the other. There was no significant effect of learning condition on the likelihood of subjects to flip the see-saw by any method (χ^2=0.23, *df*=1, *p*=0.631, *OR*=1.66). Analysis of the odds ratio between conditions showed that subjects who experienced the human learning condition were 66% more likely to flip the see-saw on a given trial, compared to subjects who experienced the object learning condition (see Figure 6.3). The effect of trial was not significant; subjects' overall likelihood to flip the see-saw did not change across trials.
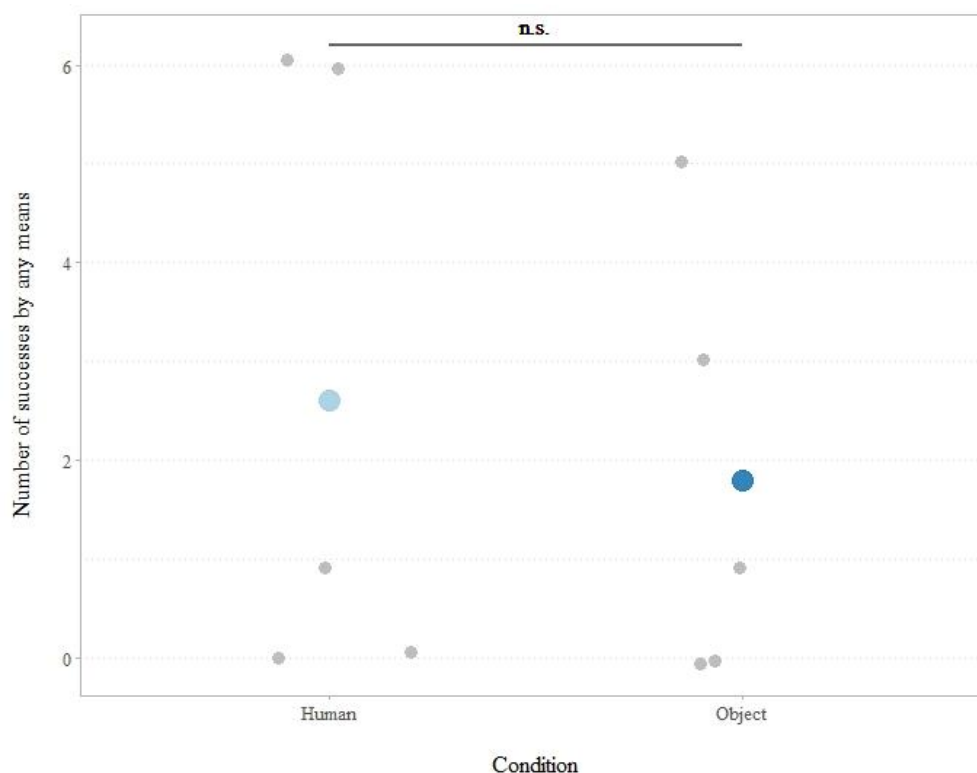
Figure 6.3 Mean number successful trials (trials in which the subject flipped the see-saw) out of twelve test phase trials, separated by learning condition. Grey dots represent the total number of flips for each individual in each group.

In analysis separating the two methods of flipping, there was a significant effect of condition (χ^2=23.27, df=1, p<0.001). The "proper" flipping method occurred only in subjects who experienced the human learning condition, while the "alternative" flipping method occurred primarily in subjects who experienced the object learning condition, with the exception of one subject in the human condition, who used alternative means to flip the see-saw on one trial (see Figure 6.4 and Figure 6.5).
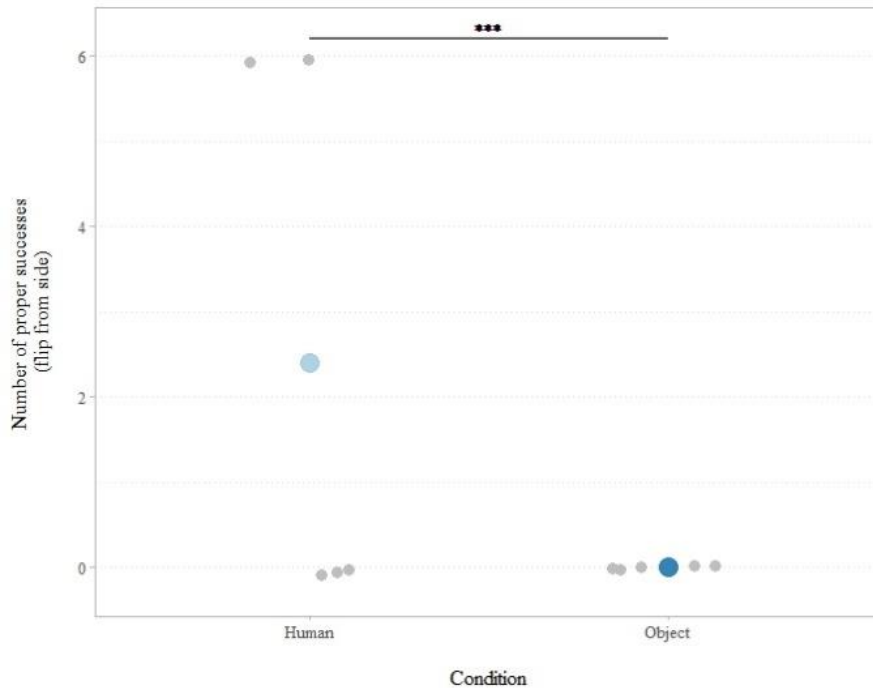
Figure 6.4 Mean number of "proper" flips separated by learning condition. Grey dots represent individual total number of "proper" flips in each condition. ***p<0.001
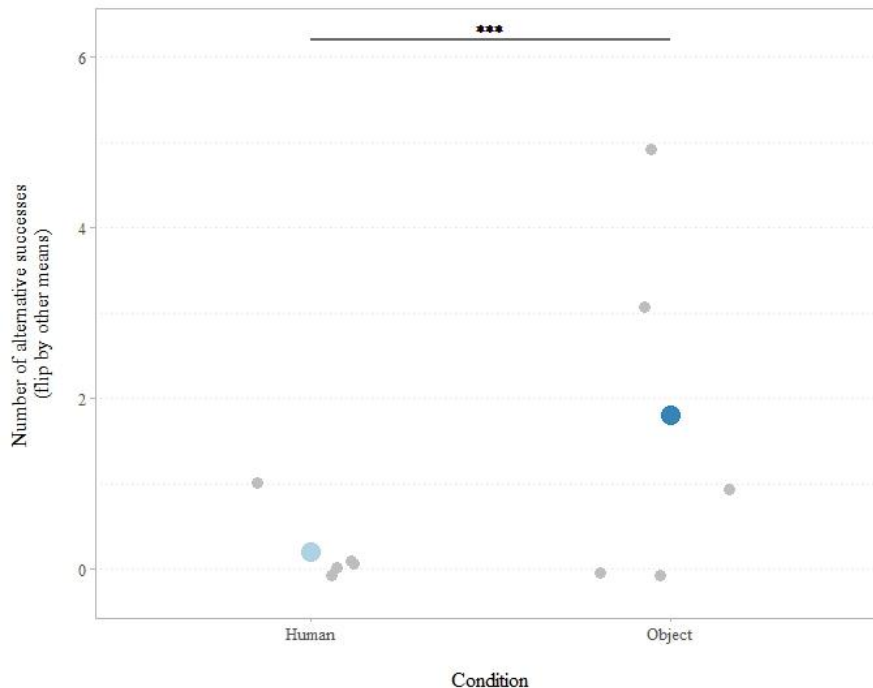
Figure 6.5 Mean number of "alternative" flips separated by learning condition. Grey dots represent individual total number of "alternative" flips in each condition. ***p<0.001

Communication

    Test Phase

Subjects produced a mean ($\pm$ SE) of 2.60 ($\pm$ 0.18) communication behaviours per trial in the test phase. There was no significant main effect of condition (χ^2=0.23, df=1, p=0.630, ER=1.09, see Figure 6.6) on the number of communication behaviours for a given trial. There was a significant effect of trial success on communication behaviours (χ^2=6.37, df=1, p=0.012, ER: 2.00); subjects produced double the amount of communication behaviours on trials where they did not ultimately flip (unsuccessful trials) than successful trials. There was no effect of trial number; subjects' rate of communication did not change across trials (χ^2=0.68, df=1, p=0.408).
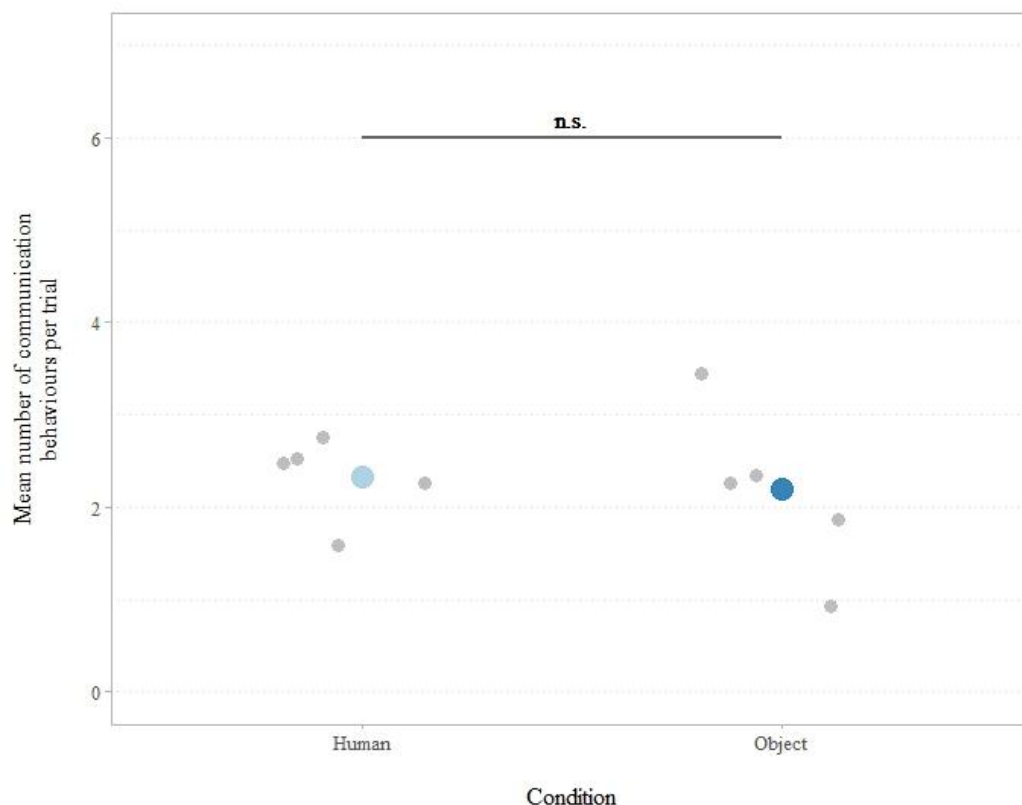
Figure 6.6 Mean number of communication behaviours per trial in the test phase, separated by learning condition. Grey dots represent the individual mean number of communication behaviours per trial in each condition.

Communication in the test phase varied significantly depending on the state of the apparatus (pre- or post-pull) (χ^2=8.76, df=1, p=0.003, ER=1.37); subjects were more likely to communicate after incorrectly pulling the paper (at which point successful use of the apparatus becomes impossible) than before pulling the paper. Analysis of the ratio of estimated mean number of communication behaviours between states of the apparatus showed that subjects produced 37% more communication behaviours after they pulled the paper than before they had done so (see Figure 6.7).
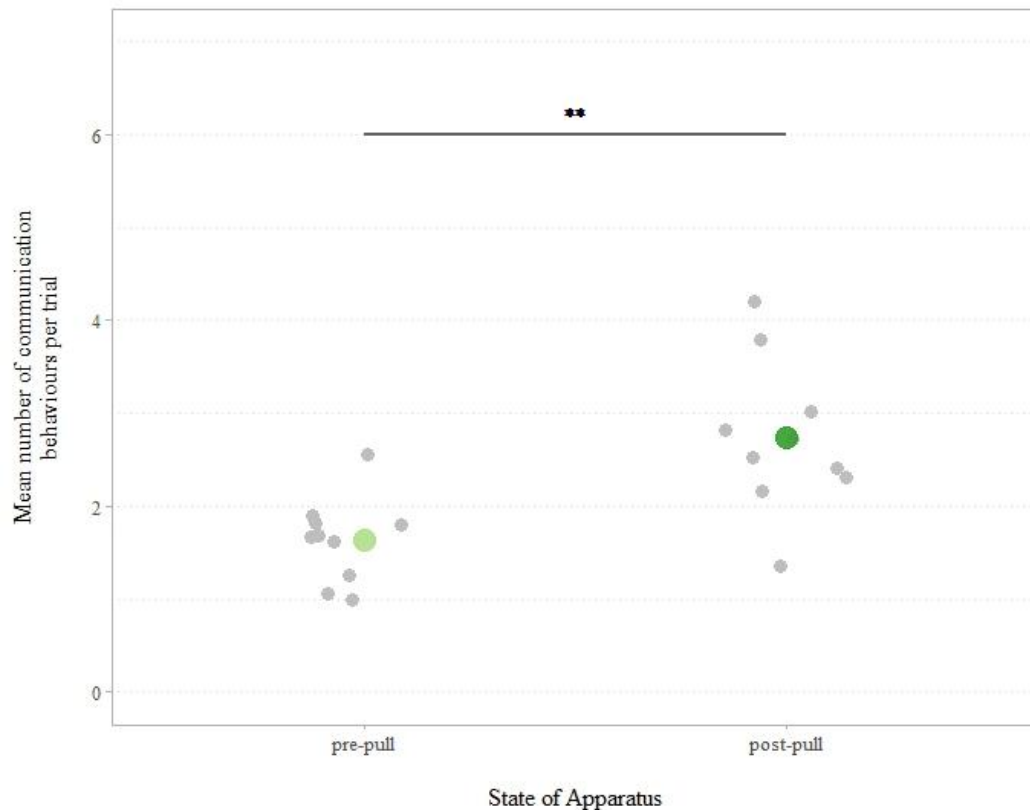
Figure 6.7 Mean number of communication behaviours per trial in the test phase, separated by the state of the apparatus (pre- or post-pull). Grey dots represent individual mean communication behaviours in for each apparatus state. **p<0.05.

Communication Phase

Subjects produced a mean (± SE) of 2.45 (± 0.15) communication behaviours per trial in the communication phase. There was a non-significant tendency toward an effect of learning condition on the number of communication behaviours per trial; subjects who experienced the human learning condition produced marginally more communication behaviours than those who experienced the object learning condition (χ^2=2.82, *df*=1, *p*=0.092, *ER*=1.36). Analysis of the ratio of estimated mean rates of communication between the two conditions showed that subjects in the human learning condition group produced 36% more communication than those in the object learning condition group (see Figure 6.8).
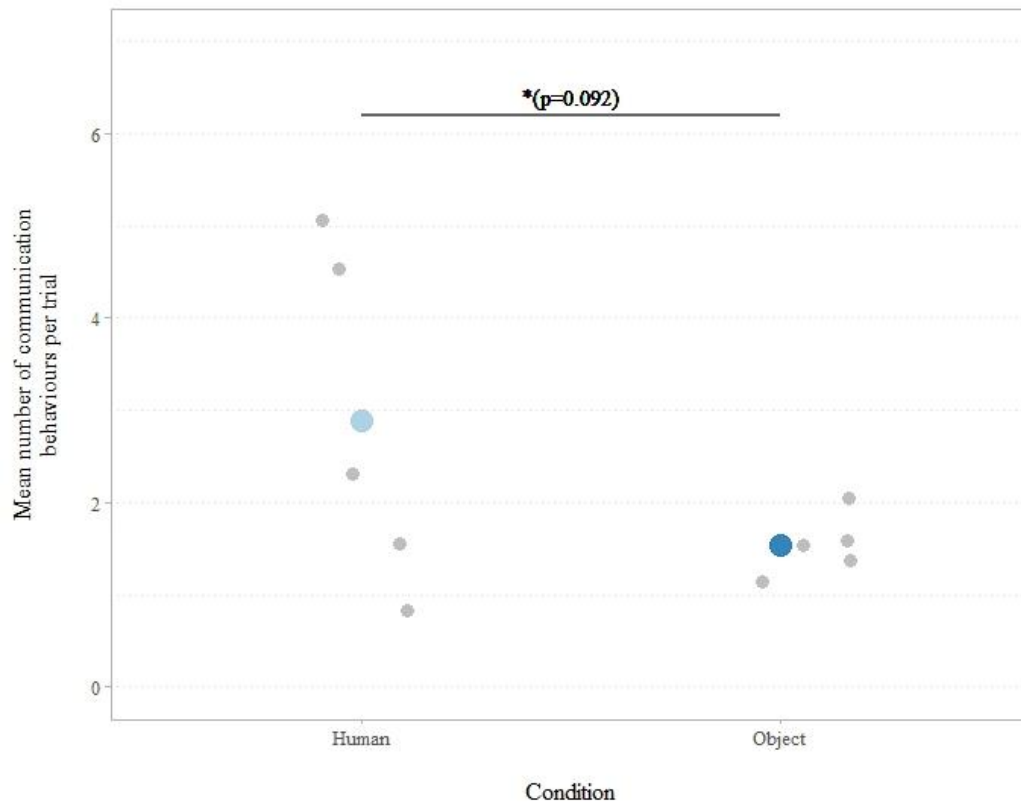
*Figure 6.8 Mean number of communication behaviours per trial in the communication phase, separated by learning condition. Grey dots represent the individual mean number of communication behaviours per trial in each condition. *p<0.1.*

There was no significant effect of trial number (χ^2=0.01, df=1, p=0.944) on production of communication behaviours in the communication phase. There was a tendency toward an effect of the state of the apparatus (pre- or post-pull) on the mean number of communication behaviours per trial (χ^2=2.71, df=1, p=0.099, ER: 1.14, see Figure 6.9), in which subjects were produced 14% more communication behaviours after incorrectly pulling the paper than before.
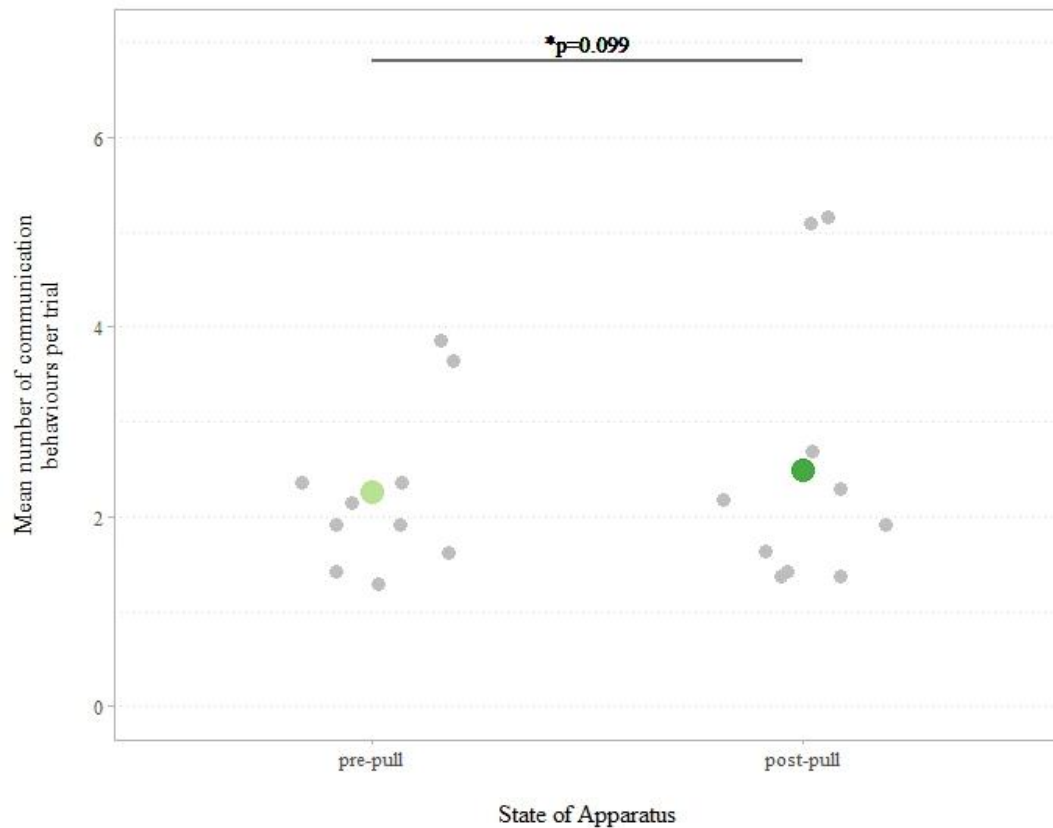
*Figure 6.9 Mean number of communication behaviours per trial in the communication phase, separated by the state of the apparatus (pre- or post-pull). Grey dots represent individual mean communication behaviours in for each apparatus state. *p<0.1*

Discussion

This study did not find strong evidence of pragmatic communication in apes within a coordination context. There is some evidence from this study to suggest that subjects' communication behaviours were driven by their own ability (or otherwise) to act on the apparatus. There is not, however, clear evidence to determine whether subjects were, in fact, communicating about the apparatus, and not merely expressing frustration induced by their perception of whether the task was solvable in each situation.

There was a non-significant tendency toward an effect of learning condition on communication in the communication phase of this experiment; there is a possible trend that chimpanzees moderated their communication behaviour based on past experience with a cooperative partner. In this phase, the subject could not flip the see-saw, and had to wait for me to do so before they pulled the paper. Chimpanzees who learned the see-saw as a coordination task with me, the human experimenter, produced more numerically more communication in this phase than chimpanzees who learned the apparatus as a non-social task with an object fulfilling my role. This tendency suggests that past experience with me cooperatively performing my role in the task (i.e., common ground as to the function of the apparatus and the roles each partner should play) may have been a relevant factor in subjects' efforts to engage my help. This is especially interesting given that there was no tendency toward this effect in the test phase, when subjects were first exposed to the breakdown of the normal function of the apparatus. The slight trend only emerged when I started (or resumed)

helping, in the communication phase. For object chimps, this was their first experience with a cooperative partner, but for human chimps, this was familiar from the learning phase, and their past experience appears to have driven a higher rate of communication. This finding should be interpreted with extreme caution, however, given that the pattern only approached significance, and may have been driven by individual subject variation. It is possible that, with a larger sample of subjects, and the subsequent increased power of the study, this effect could emerge as significant, but it is also possible that it was a result of individual differences and could be smoothed out over a larger sample. In addition to the small sample size, there are also practical limitations in the procedure of the communication phase that may have supressed the effect of learning condition. In the current design, the communication efforts from the subject made no difference to the duration of time before I flipped the see-saw for them, nor did I respond with any other changes to my behaviour. It is possible that subjects in both groups quickly realized that communication was an ineffective means to recruit my help within each trial, which could have flattened any effect of learning condition. One conceivable way to tease out this effect would be to design a condition similar to the current communication phase, but in which the experimenter is responsive to gestures and vocalizations from the subject. If subjects in the human learning condition formed a stronger expectation that I would help them with the task than those in the object learning condition, they may have been quicker and more likely to request help from a responsive coordination partner. If a difference between the learning condition groups emerged from this variation of the communication phase, it would constitute evidence that chimpanzees may, in fact, vary their communication pragmatically based on their expectations about their partner.

There is evidence to suggest that the communication in this experiment was provoked by the subjects' perceived or actual inability to act on the apparatus. In the test phase, subjects produced a significantly higher rate of communication in trials in which they were ultimately unsuccessful – trials in which they did not successfully flip the see-saw. Notably, this effect emerged even when the amount of time available in which to communicate was controlled in the model; the difference in communication is not explained by the fact that proficient flippers tended to manipulate the see-saw very early in the trial, leaving little time to communicate. This evidence suggests that subjects' communication was provoked by their perceived inability to act on the apparatus. Although it was always possible for them to manipulate the see-saw in the test phase, if they were not aware of any action they could take to do so, then they may have resorted to expressing frustration or soliciting help from me. The effect is corroborated by the finding that, in the test phase, subjects communicated more frequently after having (incorrectly) pulled the strip of paper than before having done so. The same explanation applies: while there is still an action, any action, that the subject can take on the see-saw independently, even if they understand that it is not the correct sequence of events, they are more likely to take that action than to communicate, and begin communicating only after they believe they have exhausted all of their own possible actions.

This finding is in line with existing literature on cooperative tasks showing that apes do not resort to recruitment of a partner as their first port-of-call. Hirata and Fuwa (2007) found that while chimpanzees could learn a cooperative task, they did not make any effort to solicit conspecific partners to assist them, and only solicited human partners once they learned that the task could not be solved individually. Similarly, Povinelli and O'Neill (2000), found that chimpanzees did not recruit conspecific partners using communication when presented with a task known to require coordination – they only waited near the apparatus until another individual arrived and began acting on it. The current finding is also consistent with apes' patterns of behaviour in stag-hunt paradigms, where chimpanzees have been shown to

coordinate to acquire a high-value target, discarding a low-value reward that can be acquired individually, but only under specific circumstances (Bullinger et al., 2011; Duguid et al., 2014). While apes are able to successfully coordinate their choices and choose the "stag" when the contrast in value between the two rewards is very high, and when they can easily observe the choices of their partner, they choose the individual, low-reward "hare" in situations where information about their partner's choices is not readily available; they do not resort to communication to coordinate their behaviour. The above literature seems to suggest that apes' capacity to act individually is a relevant factor in whether they will solicit help using communication, since apes do communicate with cooperative human partners in some situations. For example, Cartmill and Byrne (2007) found that orangutans solicited food rewards from human partners in an intentional, goal-directed way, including elaboration when their goals were not met, but in a task in which they were not able to produce any direct actions toward the reward themselves – the only path to the reward was communication.

The significant difference in communication between the pre- and post-pull states of the apparatus in the test phase (and the tendency toward the same in the communication phase) may reflect subjects' preference to exhaust their own actions before soliciting help. This explanation is further substantiated by the fact that I could, in terms of the logistics of the apparatus, give the subject the food reward at any time, by simply removing it from the see-saw and passing it through the mesh. Although the arbitrary rules of the task limit my help only to flipping the see-saw, the success of which is then dependent on the paper remaining in the apparatus, this is not the only action I could feasibly perform. It is plausible that subjects saw no obstacle to my helping them retrieve the food reward once they removed the paper, especially given their preference to act on the apparatus independently where possible. I believe that this speaks to an issue of arbitrary task rules similar to the task limitations I discuss in Chapter 2. Shared knowledge and mutual understanding of the requirements of a coordination task are critical for any pragmatic communication *about* the task. The expectation that apes accept the contrived rules that the human experimenter obeys actually defies what the ape knows about the task, which is that the experimenter is not functionally limited to those rules. Therefore, the necessary common ground regarding each actor's role in the task may not actually have been established, and the state of the apparatus may have been irrelevant in the ape's understanding of my ability to help. This may also have prevented any effect of learning condition – apes in both conditions may still have been more inclined to act on the apparatus themselves where possible and were equally able to see that I could still retrieve the reward for them at any point. Any effect of past experience with me helping by flipping the see-saw could have been overshadowed by my continuous ability to help without flipping the see-saw.

As in Chapter 5, the pattern of results in this experiment could not detect whether the subjects' requesting and impatience behaviours reflected pragmatic communication. There was no significant effect of past experience on communication and no clear efforts to engage my help in a specific way toward the apparatus (i.e., producing more communication pre-pull, when I could successfully flip the see-saw for them). It is therefore possible that the communication behaviours were expressions of subjects' increased frustration when they had no more actions that they could perform, or their generalized frustration at the breakdown of the formerly successful task, and not referential requests for help with the apparatus. It is equally possible that the communication behaviours were indeed intentional efforts to communicate about the apparatus, but the current pattern of results cannot distinguish between these two explanations. One way to address both the lack of common ground due to arbitrary task rules and to probe whether subjects were communicating referentially is to limit

the possible assistive actions of the experimenter. The design of this apparatus could be amended to try to facilitate an understanding of the task that is truly shared by both parties. If the apparatus could be adapted such that, after baiting, the experimenter is not able to reach the reward (e.g., the food is dropped into a transparent tube running along the slope of the see-saw and cannot be accessed until it rolls down), but is still able to flip the see-saw, it would create a situation where the experimenter's ability to help is fully dependent on the state of the apparatus. Here, the desired common ground regarding each actor's role in the task – that the only way the experimenter can provide assistance in by flipping the see-saw – is more likely to be shared by the subject. If apes are able to adjust their communication pragmatically based on common ground, then this adjusted design could produce a difference in rate of communication based on past experience, in which those in the human learning condition have a stronger expectation of help (in the form of flipping) from the experimenter and are more likely to communicate than those in the object condition. An effect of learning condition on communication, and/or pattern of communication in which apes solicit help from the experimenter while it is still possible for her to act on the apparatus, would suggest that apes are capable of communicating pragmatically about a task when they cannot conceive any alternative, non-coordination solutions. Failure to communicate pragmatically in this adjusted task would present more convincing evidence that apes do not easily use common ground and situational factors of the task to moderate their communication, as there would be fewer confounding explanations for a non-pragmatic pattern of impatience behaviours.

It is worth noting that some subjects did learn to flip the see-saw themselves in the test phase of the experiment. More than half of the subjects flipped the see-saw at least once, and four subjects flipped on multiple trials. The overall success in flipping was spread evenly across the two learning condition groups, with three successful flippers in each. There was a significant difference, however, in the flipping style between the two groups, where only those who learned the apparatus in coordination with me used their hand to flip the see-saw by pressing on the grooved side, as I did. All the successful flippers in the object condition used alternative means, such as manipulating the strip of paper as a lever to bring the see-saw into its necessary end-state with the grooved side down. I interpret this difference as evidence that although many of the subjects were able to replicate the necessary, flipped end-state of the see-saw, certain subjects in the human condition did benefit from observing my actions when I was their coordination partner. Their observation of my actions appears to have then informed their solution for the see-saw, a solution which was not innovated by any subject who did not experience the learning condition as a cooperative task. I believe that this finding supports the argument that some subjects in the human condition did not focus solely on the function of the apparatus but attended to my actions as a fellow agent in the interaction. Given the small sample of subjects involved in this finding (six of the full sample of ten, and only two who innovated the "hand" flipping method), this result should be interpreted with caution. It is a promising finding, but the sample size is too small to assess the effect of flipping style on communication efforts, for example, or to allow general predictions about chimpanzee action-learning within coordination based on this experiment.

This experiment used a novel task to examine communication with a human partner in the context of coordination, one in which both the cooperative human and the subject take an active role in manipulating the apparatus. In that sense, it is a useful task for probing communication used to coordinate while staying in the bounds of ontogenetically developed behaviours for chimpanzees. Their communication in this paradigm needed only be imperative, which lifted the requirement that the apes step outside of their ontogenetic

constraints to declaratively transmit information for a coordination goal, while still probing the flexibility and informative intentions of that communication (see Halina et al., 2018, for an example and discussion of chimpanzees flexibly adjusting their imperative pointing gestures based on context; relatedly, see Povinelli & O'Neill, 2000, for a null finding toward apes declaratively instructing coordination partners; see Hopkins et al., 2013, for a critique of declarative paradigms). At the same time, the required action from the experimenter is more than just transferring food or an object – it is a specific motor action that is related to the one the ape must then perform, which offers the opportunity to assess whether the ape is communicating *about* that action (with an informative intention). This is particularly true with modifications addressed above, such as adaptations to the apparatus that prevent any other type of helpful action from the experimenter. This design could be amended to produce various contexts of common ground (or lack thereof), necessity of coordination, and specific required actions to further probe the degree to which apes will communicate pragmatically in a coordination context. For example, apes in the coordination condition could be compared to apes who observed the function of the see-saw in a social learning context, where the experimenter demonstrates the flipping, and then the subject receives an unrelated reward. This would juxtapose the effects of mutual past experience with representation of the knowledge state of the experimenter – in both situations, the experimenter has demonstrated competency with the apparatus, but has only been construed as a coordination partner in one context. Examining any difference in rate of communication between these two groups would allow for a fine-tuned examination of the apes' use of common ground when they request help – whether apes differentiate between common ground related to knowledge and common ground related to joint action.

This paradigm could also be leveraged to examine sensitivity to ostension through the lens of natural pedagogy, using action-learning as a measure of comprehension. Natural pedagogy views ostension as a vehicle for the transmission of relevant information, especially in a teaching context (Csibra & Gergely, 2009). Here, it would be possible to compare variations on the coordination condition, one with an ostensive display prior to the experimenter flipping the see-saw, and one with an attention-getting, but non-communicative display, as in Chapter 4. Rather than using gaze-following or communication as a measure of sensitivity to ostension, this paradigm could examine the rate of practical acquisition of the flipping motion, controlling for attention and stimulus enhancement, to determine whether ostension primes subjects to view the experimenter's actions as relevant, pedagogical, and informative.

The interpretation of the results in this study is limited by its small sample size, particularly in that certain models could not account for individual variation between subjects as a random effect. For example, it was not possible to include subject as a random effect in the model comparing flipping between conditions, due to the lack of within-subject variation in flip style, and it is not possible to know, with a subset (flippers) of a 10-subject sample, whether this effect is driven by condition or by individual variation. It would be beneficial to replicate and expand this study with additional populations of apes, to build power in the analysis and smooth out individual variation. This study is also narrowed by the fact that ape subjects are more likely to solicit help from a human experimenter than from a conspecific in cooperative tasks (Chalmeau et al., 1997; Hirata & Fuwa, 2007), which limits the ecological validity of its findings. This paradigm does not answer questions about the extent to which apes account for shared past experience in their intraspecific social interactions. If it were possible, it would be fascinating to expand on this design with a similar concept that could be implemented between two chimpanzees, where only one is knowledgeable about and able to access the see-saw, to flip it. This would permit the other chimpanzee, the producer, to stay in

the domain of imperative requesting, but would probe whether they vary their communication for a conspecific partner based on past experience of coordination. If the above design with an adjusted apparatus (blocking the experimenter's direct access to the food reward) were compared to the same paradigm between conspecifics, this could answer empirical questions about the limits or conditions under which chimpanzees will and will not request help – is any partner solicitation unique to their interactions with humans, or is it dependent on the type of information they must transfer? Yamamoto et al. (2009) found that chimpanzees made imperative requests for tools and conspecific partners were willing to give them, in a cooperative context, so it is possible that certain experimental circumstances could facilitate conspecific partner recruitment. The current paradigm is only the start to a line of inquiry about primate inferential communication in coordination contexts, but it is rich with potential for further distinctions between the nuanced cognitive mechanisms that underlie this process.

Chapter 7 General Discussion

Introduction

I now turn to a general discussion of the experiments and ideas presented in this thesis. I first summarize the key findings from each chapter and contextualize them with their empirical and theoretical implications for the study of pragmatic communication in non-human primates. In this section, I review the strengths and weaknesses of the practical orientation of this work, and I situate my findings within the existing theories of ostension and pragmatics. Finally, I discuss potential future directions for this program of research, which would expand and elaborate upon the current findings to explore increasingly nuanced elements of the cognitive processes underlying pragmatic communication in non-human primates.

Summary of Key Findings

This work investigated non-human primates' capacity for pragmatic communication, including ostension. I assessed sensitivity to communicative intention from a comprehension standpoint, and the ability to adjust communication based on past experience or task demands from a production standpoint. One of the aims of this program of research was to examine these questions using methodology with a bottom-up framework, focussing on existing natural behaviours within the primate repertoire and attempting to measure their capacity for ostension by manipulating those behaviours and biases. Using this approach, I identified some evidence of sensitivity to ostension in primates, most notably when the parameters of the task and the measures of ostension are based around the violation of primates' expectations, rather than their ability to report their understanding of a specific, semantic message.

In Chapter 2, I examined whether chimpanzees moderated their object choice patterns based on their differentiation between ostensive and non-ostensive displays from me, a cooperative human partner. The results of this experiment did not support the hypothesis that chimpanzees were sensitive to the relevant and information-bearing nature of ostensive communication; the subjects did not modify their choices in favour of the ostensively-displayed choice. However, theoretical and empirical weaknesses in the design of this task suggest that this finding may not be an appropriate measure of sensitivity to ostension in non-human primates. This task did not follow the bottom-up approach of later investigations, rather, it was designed to parallel a functionally identical task conducted with infants, and it assessed primates' comprehension of communicative intention using a solicited and trained reporting behaviour: pointing to one of two choices. As I have discussed in previous chapters, I believe that the expectation that chimpanzees interpret correct semantic meaning (i.e., "the food is here") from human behaviour, when the information is conveyed declaratively, is not a valid measure of their comprehension of ostension. There are too many confounding factors to rule out sensitivity to ostension: first, declarative communication, or sharing information prosocially, is not part of normal ape ontogeny (Lyn et al., 2010; Tomasello, 2008b). Even if they have experienced declarative utterances from human experimenters before, they may lack the common ground to assume that the information is for them, and thus do not draw the inference that it conveys the location of the food, even if they understand that they are being communicatively addressed. Second, the subject's role in this task was a passive one, which presented no real motivation to attend to the actions of the experimenter, especially since the

task was indiscriminately rewarded, and their attention to me had no bearing on the outcome of the trial – they always received the food. Common ground in terms of expectations about an exchange and each agent's role in it are vital for successful comprehension of ostension – without it, the communication will fail whether or not the subject receives the communicative intention. My assessment of the limitations of this study is in line with both established (e.g., Hopkins et al., 2013) and recent theoretical work on ostension (Melis & Rossano, 2022), which agree that paradigms like this one, with asymmetrical common ground, are an inefficient line of inquiry into ostension in non-human primates.

In order to give language to the flexibility and complexity in non-human primate communication that, in my opinion, extends beyond purely intentional, goal-directed communication, but does not show any specific markers of ostension (i.e., production or comprehension of communicative intention), I explored pragmatics and inference from a theoretical perspective in Chapter 3. Here, I presented a lens through which to view primates' flexibility in communication – they have the capacity to make inferences about the goals, knowledge states, and motivations of others, and the extent to which they apply this ability in their communication behaviour merits investigation. While non-human primates may or may not make their social inferences manifest to their communicative partners, as they might in full-blown ostensive communication, they may use their inferences to inform their own production and comprehension of communicative acts. A recent investigation of primate communication using computer modelling reaches a similar conclusion; they suggest that primates may draw on their general capacity for pragmatic reasoning to integrate contextual factors when they interpret communication – essentially capitalizing on their social inferences (Bohn et al., 2022). In this chapter, I concluded that primates may engage with informative intention, and use context to draw relevant inferences about it, without necessarily involving communicative intention, thus engaging in "inferential communication," or the pragmatic interpretation of others' social and communicative behaviour. I propose, from this theoretical analysis, that pragmatic communication can be examined in primates by harnessing the flexible behaviours that they already produce, and especially by attempting to moderate the biases and assumptions that they have been shown to make about other agents, rather than deriving methodology solely from expectations based on the human experience of ostension.

With the bottom-up framework of inferential communication in mind, I designed the study presented in Chapter 4, in which I investigated whether primates acquired an expectation of relevant information when they were addressed with ostensive communication, using their gaze-following behaviour as a measure. The results of this experiment showed that primates moderated their gaze-following behaviour in response to ostension, suggesting that ostensive behaviour did increase their expectation of the relevant information normally contained in gaze. This experiment also ruled out simple enhanced attention as a driver of this effect and provided evidence that primates have the capacity to comprehend communicative intention when the demands of the task account for the constraints of their ontogeny. This task did not solicit any behaviour from the subject; it measured a naturally occurring and untrained reaction. Furthermore, it did not demand that the subjects acquire any specific information in order to report their comprehension of communicative intention – they needed only be surprised that there was not any information to obtain. These two factors taken together may have mitigated the incomplete common ground between me and the primate subjects – they did not need to draw any specific inferences in order to show a behavioural response to communicative address. I take these findings as evidence that primates do form some expectation of relevance in response to ostension.

I built on this finding in Chapter 5, where I further explored the effect of ostensive address on great apes' expectation of action from a human partner, measured by their production of impatience and requesting behaviours. In this experiment, I used varying emotional valences within my ostensive displays, in order to examine whether apes are sensitive to the context-setting nature of emotional tone in communication. The results showed that apes do produce different rates of communication in response to ostensive displays with different emotional valences, suggesting that emotional context does moderate their behavioural responses in communicative exchanges. This suggests that the effect of ostension is subject to moderation by other factors in a communicative exchange, such as tone. This experiment was unable to determine, however, whether the change in rate of communication was moderated by context-dependent comprehension of communicative intention or by the reactive emotional state of the subject. Regardless of the driver of the behaviour, this experiment demonstrated that emotional valence is a relevant factor in communicative exchanges with primates and should be taken under consideration when designing displays and interpreting results induced by communicative displays. This experiment also found a difference in rate of communication according to the distraction state of the experimenter, suggesting that the subjects' production of impatience and requesting behaviours was moderated by their reaction to either my state of occupation or their perception of their access to my attention. As with the effect of emotional valence, it is not clear from these results whether this effect was driven by their own moderated feelings of frustration, or by their comprehension of the situational factors in the communicative exchange. I view these findings as further evidence that ostension can be assessed through changes to naturally occurring, unsolicited behaviours, but caution that future designs using rate of communication as a measure should control for the effect of frustration, which would enable a richer and more nuanced understanding of the cognitive mechanism driving any change in the rate of behaviour.

In my final experiment, detailed in Chapter 6, I examined whether chimpanzees produced impatience and requesting behaviours pragmatically depending on their past experience with me as cooperative partner. The results did not support the hypothesis that subjects would recruit the help of a cooperative partner more often if they had past experience of coordination with that partner, and did not, therefore, find evidence of pragmatic communication in chimpanzees. As with the study in Chapter 5, it was difficult to separate the effects of frustration or generalized protest at the breakdown of the normal function of the apparatus from true communicative attempts to request help in the form of coordination. The findings from this study supported existing literature showing that chimpanzees do not generally resort to coordination when there are individual actions still available to them (e.g., (Hirata & Fuwa, 2007). This finding complements studies where apes have been shown to use communication to sustain coordination, but only in situations where they had no actions available to them and could only proceed if the coordinating partner performed their role (e.g., Voinov et al., 2020). I believe that the findings from this study raise an important discussion about task validity from the perspective of the non-human subject. In this study, apes were not sensitive to past experience of my help, nor did they keep their communication to situations where my acting on the apparatus would be helpful toward their goal. However, both these distinctions between contexts (past experience and task demands, respectively) are predicated on the idea that I could only help by flipping the see-saw, which was not truly the case. In my opinion, this raises a similar asymmetry of common ground to the study detailed in Chapter 2: my perspective on the assumptions that the subject should make about the task were based on my own willingness to adopt and follow arbitrary task rules, a propensity that I

should not necessarily have ascribed to non-human primates. Although I believe that the apparatus designed for this task is a useful one to probe communication in a coordination setting, the task should be adjusted such that the subject's perspective on the ways in which the experimenter is able to act on the apparatus is accurate – the experimenter should be truly, and not arbitrarily constrained in their actions.

Overall, the work presented in this thesis finds some compelling evidence for sensitivity to ostension in non-human primates – specifically, that it is possible to moderate certain primates' expectation of information using ostensive behaviour. In terms of existing theories of ostension, this effect is situated in both relevance theory and natural pedagogy, in that the subjects appeared to form an expectation of relevant information in response to communicative address, and thus followed the expected pattern of presumption of relevance triggered by the comprehension of communicative intention (Sperber & Wilson, 1986; Wilson & Sperber, 2002; Csibra & Gergely, 2009). To further describe this effect in terms of natural pedagogy, it is possible that the ostensive display modified the subject's cognitive environment, priming them to expect a relevant referent and creating a sense of "prosocial promise" that any subsequent behaviour is provided *for them* (Csibra, 2010). This "promise" manipulates the subject's expectations of information, action, or any other relevant referent, and can cause behavioural change. This effect that has not generally been detected in past choice paradigms with non-human primates (although see Marno et al., 2022 for a paradigm measured by object choice, but in which ostension moderates social learning, not semantic meaning). A similar effect has been observed, however, in experiments with canines, where ostension moderated their expectations about the location and contents of target objects, also interpreted through the lens of natural pedagogy (Tauzin et al. 2015a,b).

This work also found that any potential effects of ostension on primates' expectations or behaviour are subject to moderation by factors such as emotional tone. This raises an important and understudied consideration in communication research: stimuli must be evaluated for their emotional impact, in order to truly tease out the effects of communicative intention. This line of research also provides some evidence that the behavioural outcomes of ostension are a useful means of measuring sensitivity to communicative intention. As in the theory of natural pedagogy (Csibra & Gergely, 2009) ostension may moderate existing cognitive biases, and I believe that natural behaviours and biases are rich with potential for further investigation into the comprehension of ostension in non-human primates.

These studies do not fund substantial evidence for the production of pragmatic or ostensive communication – it was either not possible to differentiate between referential communication and expressions of frustration, or the communication did not vary according to pragmatic factors. Production of pragmatic and ostensive communication is more difficult to assess via the manipulation of expectations or biases, and it is more difficult to find comparable markers of production of ostension between species, where the body language and gestures may not be shared. It is a question that merits further theoretical and empirical consideration. In addition to the modifications proposed to tasks in relevant chapters to differentiate between frustration and intentional, referential communication, I detail two possible lines of inquiry into production of ostension, below.

Proposed Future Directions

There are several possible routes by which to continue and expand this line of research into pragmatic and ostensive communication in non-human primates. In the above section, I highlight some overarching methodological considerations for research into communication cognition in animals. In general summary, the work presented in this thesis could be expanded and elaborated by continuing to search for behavioural measures of sensitivity to ostension such as naturally occurring reactive behaviours, existing cognitive biases, and established social expectations. Likewise, I propose that future tasks examining ostension and pragmatic communication in non-human primates take care to evaluate and control the effects of factors like emotional valence, which may otherwise exaggerate or disguise any effects of ostension. I also note the importance of the nature of information carried in any ostensive stimuli – if a specific message must be acquired, the ontogenetic development of non-human primates may require that the information be imperative, rather than declarative, in order to maintain common ground regarding the purpose of communicative interactions. Finally, I suggest cautious examination of presumed common ground and presumed validity of the parameters of experimental tasks, to ensure that common ground is not asymmetrical between human experimenters and primate subjects, which may, again, hinder the assessment of any effect of ostension.

The work presented in this thesis did not directly assess primates' production of ostensive communication and also found no unequivocal evidence of pragmatic communication in non-human primates. In order to delve into behavioural measures of pragmatics and ostension from the production standpoint, I believe it is equally important to use untrained responses and to use paradigms that provoke a change in behaviour, rather than a tendency toward a specific choice. One area which I have not explored, that I believe could expand my current line of inquiry, is analysis of the type and modification of communicative signals. I propose two possible areas for experimentation – the first is to analyse whether, in paradigms like the ones presented in Chapter 5 Chapter 6, where the subjects are producing a variety of communicative behaviours, the type of signals (e.g., auditory/visual, percussive versus bodily movement, etc.) varies between conditions. For example, would apes, presented in turn with a knowledgeable or naïve experimenter, change their style of communication to solicit coordination, if they were inclined to do so at all? Such a distinction between the knowledge states of the experimenters – both may be presumed to be willing to help, but only one knows what to do – would be evidence that the subjects can account for the knowledge state of another, and moderate their communication accordingly, which would constitute pragmatic communication.

A second potential paradigm investigating modifications to communicative signals is an examination of the "shape" or placement of the signals. In this framework, one would measure whether apes are capable of varying the manner in which they produce the same signal, according to context. There is some existing work on this question: Tauzin et al. (2020) found that both apes and human children modified the shape of their pointing gesture to disambiguate between two spatially ambiguous options. While this experiment does use pointing as a measure, which is not necessarily a naturally occurring behaviour, it is measuring untrained changes to the way that trained behaviour is produced, which, in my view, is still a measure of behavioural change in order to communicate pragmatically. I propose a similar experiment, in which the distance between a single high-value and several low-value food rewards is varied, such that the high-value food reward is sometimes very close to other, low-value ones (spatially ambiguous) and sometimes very far away from any other food option (spatially unambiguous). In this experiment, the measure of pragmatic communication is the placement of the selection (pointing or reaching) gesture. If subjects do

not vary the placement of their pointing gesture, it would suggest that they are not engaging with the mental state of their recipient and are either insensitive to the potential to be misunderstood, or are producing the selection gesture not as a referential point, but as an aborted reach. If primates vary their placement of the gesture to be more precise when the options are spatially ambiguous, from a baseline of precision when the options are spaced unambiguously, it would be evidence that they take the recipient's likelihood of comprehension into account – a sign of pragmatic communication. Like the experiment by Tauzin et al. (2020), this would probe for a spontaneous modification to a trained behaviour, which falls into the category of untrained reactions to contextual factors affecting communication. Flexible production of gestures, not just in terms of selection and/or suppression of gestures, but also regarding the manner in which they are produced, could constitute behavioural evidence for production of communicative intention – the subject knows that their communication is *for* the recipient, and modifies their signals according to their partner's physical or mental state.

Concluding Remarks

The cognitive mechanisms of pragmatic communication are a complex and nuanced puzzle, and the study of ostension and pragmatics in non-human primates, even more so. In this thesis, I present some evidence that primates are sensitive to the information-bearing nature of ostension, and that their expectations and behaviour can be moderated by communicative intent. Along with other recent examples of sensitivity to ostension in primates (e.g., Marno et al., 2022), these findings suggest that there is richness and flexibility yet unexplored in the realm of primate communication. I believe that the question of the extent to which non-human primates engage in inferential, mentalized communication deserves careful consideration, and deeper further study, especially in paradigms which account for the ontogenetic differences between human and non-human primates, and which modify their task parameters accordingly. I hope to continue this line of inquiry into non-human primate communication, both personally and through future collaborations, to seek an increasingly precise understanding of the processes that underlie primates' complex social behaviours.

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Appendices

Appendix A: Species Housing and Food Reward Information

Details of the location, housing conditions, group arrangement, and permitted high-value food rewards for each primate group investigated in this study are given in the table below.

Group	Location	Group Size	Individuals Tested*	Testing Locations	Group Arrangement	High-Value Food Reward
Orangutans	Twycross Zoo	5	5	beds	fission-fusion (3+2 or 4+1)	sweet potato
Gorillas	Twycross Zoo	6	6	beds	one group	sweet potato
Bonobos	Twycross Zoo	13	10	beds	fission-fusion (6+7 or 5+8)	sweet potato
Chimpanzees (Twycross)	Twycross Zoo	14	8	beds	two groups (3 and 11)	sweet potato
Chimpanzees (Edinburgh)	Edinburgh Zoo	15	12	BRU	one group	whole or half grapes
Siamangs	Twycross Zoo	3	3	beds	one group	half grapes
Buff-Cheek Gibbons	Edinburgh Zoo	3	3	outdoors	one group	carrot
Capuchins	Edinburgh Zoo	37	25	research cubicles	two groups (17 and 20)	raisins

*total number of individuals within the group who participated in any of the four studies

Appendix B: Details and Images of Research Areas and Arrangements

Appendix B1. Bird's eye view image of the Budongo Research Unit (BRU) with relevant research areas and research panels labelled. "Research Area" indicates areas where human researchers can safely sit or stand to conduct experimental research with the chimpanzees at Edinburgh Zoo. All research areas are separated from chimp areas by metal walls or by mesh/polycarbonate panels (numbered 1-11 below). "Chimp Area" indicates areas where chimpanzees can enter or exit freely during research times. These areas are accessed via one of the chimpanzee's indoor enclosure pods (Chimp Pod No. 1), and are divided by hydraulic doors (H1, H2, and H3), which are always open during research times. The experiments in this study were conducted with the Edinburgh chimpanzees at the following panels: Chapter 2 – panel 6; Chapters 4 and 5 – panel 8; Chapter 6 – panels 7, 8, and 9.
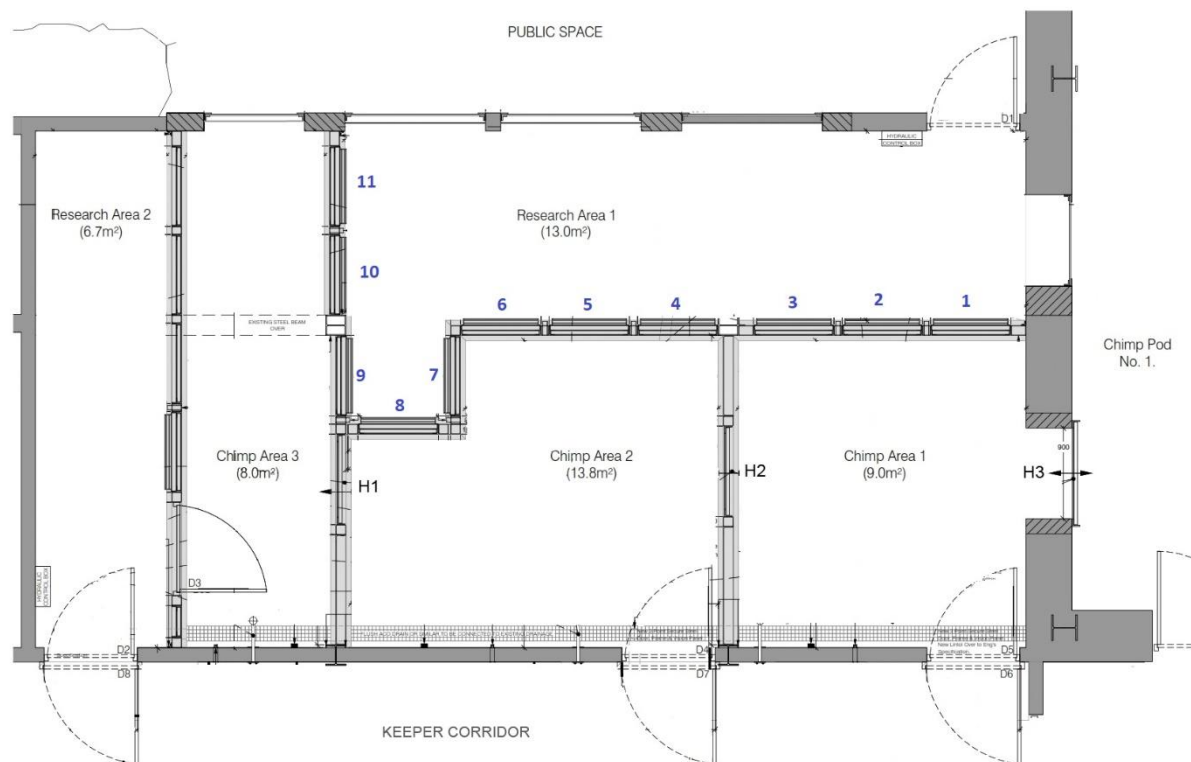
Appendix B2. Image of panel 6 (see above) fitted with a polycarbonate window offering three choice holes. The panels in the BRU measure 88cm by 78cm, and the choice holes are 3cm in diameter. The panel in this image is equipped with the polycarbonate shelf used in the experiment in Chapter 2.

Appendix B3. Image of the alcove in the BRU containing panels 7-9, at which the experiment described in Chapter 6 was conducted.

Appendix B4. Image of the orangutan testing area (beds) at Twycross Zoo (left) and an up-close image of a subject in the orangutan testing area (right).
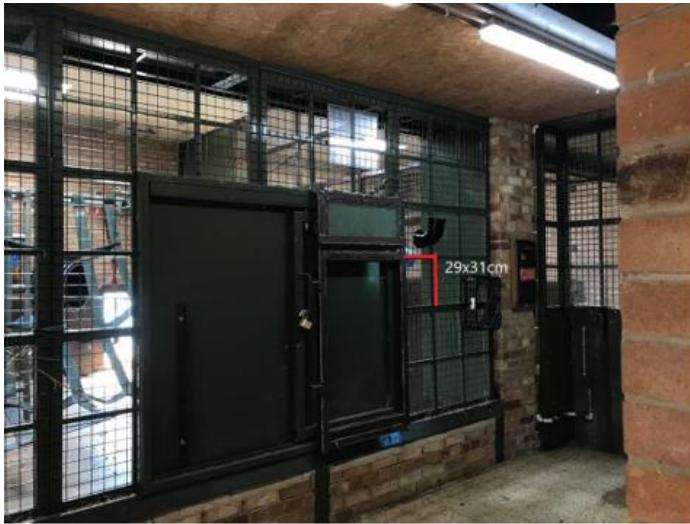
Appendix B5. Image of the gorilla testing area (beds) at Twycross Zoo

Appendix B6. Image of an up-close view of a subject in the bonobo testing area (beds) at Twycross Zoo (left) and an angled view of the bonobo testing area (right).

Appendix B7. Image of the chimpanzee testing area (beds) at Twycross Zoo

Appendix B8. Image of the siamang testing area (beds) at Twycross Zoo (left) and up-close image of a subject in the siamang testing area (right).

Appendix B9. Image of the buff-cheek gibbon testing area (outdoor wall of the enclosure) at Edinburgh Zoo. Text denotes the mesh panel where research occurs.

Appendix C: Supplementary Statistical Information for Chapter 2: Proto-Presumptions of Relevance in Chimpanzees

Appendix C1. Table of exact binomial test results for individual proportion of choices to the ostensively displayed side in both the baby-same and the chimp-friendly conditions. Binomial tests were conducted with a hypothesized chance value set to 0.5 (50% ostensive) and a 95% confidence interval. No subject deviated from chance in their choices to the ostensively displayed side.

	Baby-Same		**Chimp-Friendly**	
	% Ostensive	*p-value*	*% Ostensive*	*p-value*
Velu	41.67	0.774	41.67	0.774
Frek	66.67	0.388	50	1.000
Qafzeh	50	1.000	50	1.000
David	50	1.000	58.34	0.774
Louis	50	1.000	50	1.000
Lucy	58.34	0.774	41.67	0.774
Kilimi	50	1.000	50	1.000
Tupelo	58.34	0.774	66.67	0.388

Appendix C2. Table of exact binomial test results for individual proportion of choices to a single side in each of the three experimental conditions. Binomial tests were conducted with a hypothesized chance value set to 0.5 (6 out of 12 choices to a single side) and a 95% confidence interval. Almost all subjects selected a single side at a rate significantly above chance in all conditions (≥ 10 choices to a single side); those that were not significantly above chance showed a strong trend toward their preferred side in all conditions. * p <0.05, **p<0.001

Subject (preferred side)	**Baby-Same**		**Chimp-Friendly**		**Control**	
	# Choices to preferred side	*p-value*	*# Choices to preferred side*	*p-value*	*# Choices to preferred side*	*p-value*
Velu (L)	9	0.146	9	0.146	11	0.006*
Frek (L)	10	0.039*	12	<0.001**	11	0.006*
Qafzeh (L)	10	0.039*	8	0.388	12	<0.001**
David (L)	12	<0.001**	11	0.006*	12	<0.001**
Louis (L)	10	0.039*	12	<0.001**	12	<0.001**
Lucy (R)	11	0.006*	11	0.006*	11	0.006*
Kilimi (L)	10	0.039*	12	<0.001**	12	<0.001**
Tupelo (R)	11	0.006*	10	0.039*	12	<0.001**

Appendix D: Supplementary Statistical Information for Chapter 4: Mediating Gaze-Following and Double Looks with Ostensive Behaviour

Appendix D1. Table of GVIF values to assess multicollinearity in each GLMM of this analysis. Multicollinearity was not a concern in any model; all GVIF values were below 2. Note that all models included only the data from the first half of each session, apart from the preliminary double looks GLMM, which included all trials.

Variable	Double Looks (all trials)		Display Attention		Looking Attention		Initial Looks		Double Looks	
	GVIF	*df*	*GVIF*	*df*	*GVIF*	*df*	*GVIF*	*df*	*GVIF*	*df*
display type	1.0002	2	1.0002	2	1.0002	2	1.0002	2	1.0014	2
age group	1.0001	2	1.0001	2	1.0001	2	1.0004	2	1.0000	2
session	1.0001	1	1.0000	1	1.0000	1	1.0005	1	1.0014	1
trial within session	1.0000	1	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a

Appendix D2. Table of pairwise comparisons between display types within the GLMMs for display attention, looking attention, and initial looks. There were no significant differences between each of the display types on any of these measures.

Comparison	Display Attention			Looking Attention			Initial Looks		
	z-value	*df*	*p-value*	*z-value*	*df*	*p-value*	*z-value*	*df*	*p-value*
ost – attn	0.412	1	0.911	-1.190	1	0.459	1.777	1	0.177
ost – ctrl	1.872	1	0.913	-0.351	1	0.934	1.342	1	0.372
attn – ctrl	1.461	1	0.963	0.840	1	0.678	-0/440	1	0.899

Appendix E: Supplementary Methodological and Statistical Information for Chapter 5: The Effect of Emotional Valence within Ostensive Behaviour on Apes' Expectation of Action

Appendix E1. Detailed ethogram for identification and discrimination of communication behaviours; this exact ethogram was provided during training for reliability coding.

Behaviour	Definition
tap	the subject taps or raps their fingers or hand against the table, window, mesh, or feeding tube. Taps may be single or repetitive and should be counted only once if the subject has not removed their fingers from the mesh in between taps. Note that a tap or contact between the fingers and the apparatus performed as part of an action to extract food from the feeding tube, window, or mesh, should not be counted
finger thrust	the subject thrusts their fingers (or single finger) through the mesh. Thrusts may be single or repetitive and should be counted only once unless the subject completely ceases the action (either by removing the fingers entirely or by leaving the fingers through the mesh passively) and then subsequently begins again. Protrusion of the fingers through the mesh in the act of tapping should not be counted.
head nod	the subject moves their head up and down (nodding) or side to side (shaking, i.e., ear moves toward shoulder) repeatedly (at least two movements) with the eyeline directed at the researcher.
hand fling	the subject raises their hand upward and produces a flinging gesture toward the shoulder
present mouth	the subject presents their lips/mouth, open or closed, such that at least one lip protrudes through the mesh. Note that the use of the lips, tongue, or teeth to extract food from the feeding tube or windowsill should not be counted.
clap	the subject claps their hands together. This gesture may be single or repeated but should only be counted twice if the behaviour fully ceases before beginning again.
tap body	the subject taps their fingers or hand against their own body, usually on the head or chest. Taps may be single or repetitive and should be counted only once unless the motion completely ceases and then starts again. Gorillas beating their chests in the direction of the researcher (but not toward others in play) should be counted.
pass object	the subject pushes or holds and object through the mesh either partially or completely. All motions/thrusts/taps associated with this activity should be counted as one event unless they completely cease the behaviour (1 second elapses between efforts or the subject engages in another behaviour and then returns to this behaviour) and then resume while the object is still partially in the mesh - options: paper; stick; substrate (e.g., wood wool, grass, wood chips); other
present body	the subject presents a part of the body by pressing it forward against or through the mesh or feeding tube apparatus - options: chest; back; genitals/bum, shoulder, foot
grumble	the subject produces an audible, low-pitched vocalization, akin to a grunt, grumble, or cough (coughing due to illness should not be counted). Low pitched vocalizations as part of a display should not be counted.
raspberry	the subject produces a lip buzzing/raspberry sound/mouth gesture. This sound/gesture may be single or repeated but should only be counted twice if the behaviour fully ceases before beginning again.
spit	the subject spits in the direction of the researcher - options: object (the subject puts an object such as grass, nut shell, etc. in their mouth, and then spits it toward the researchers); saliva (the subject spits saliva or a mouthful of water toward the researcher)

Appendix E2. Table of GVIF values to assess multicollinearity in each GLMM of this analysis. Multicollinearity was not a concern in any model; all GVIF values were below 2.

Variable	Display Phase Model		Distraction Phase Model	
	GVIF	*df*	*GVIF*	*df*
display type	1.0001	2	1.0002	2
distraction type	n/a	n/a	1.0001	1
species	1.1568	3	1.1637	3
age group	1.1566	2	1.1636	2
session	1.0001	1	1.0001	1

Appendix E3. Table of individual rates of gesture type usage, expressed as a percentage of total number of gestures used by that individual.

Gesture represents ≥ 75% 50% 25% 1% of subject's total gestures

Subject	Species	tap	finger thrust	pass object	present mouth	present body	head nod	lip buzz	tap body	hand fling	clap	grumble	spit
Kibriah		71	18	.	4	2	.	.	.	.	.	.	5
Maliku		56	.	22	.	.	.	.	11	.	.	.	11
Batu	orangutan	41	3	24	.	.	.	.	.	.	.	3	28
Kayan		69	23	.	.	8	.	.	.	.	.	.	.
Basuki		21	26	28	.	23	.	.	.	.	2	.	.
Biddy		58	17	25	.	.	.	.	.	.	.	.	.
Ozala		45	18	36	.	.	.	.	.	.	.	.	.
Oumbi	gorilla	.	.	83	.	7	.	.	.	.	.	10	.
Lope		19	3	52	.	.	.	.	26	.	.	.	.
Shufai		58	3	32	.	5	.	.	3	.	.	.	.
Diatou		20	55	.	3	.	.	.	12	.	10	.	.
Lina		66	34	.	.	.	.	.	.	.	.	.	.
Cheka		34	61	.	.	5	.	.	.	.	.	.	.
Maringa		.	26	.	71	3	.	.	.	.	.	.	.
Likemba	bonobo	12	8	1	69	6	1	.	2	.	.	.	.
Malaika		1	10	.	87	1	.	.	.	.	.	.	.
Lucuma		10	60	.	20	.	.	.	.	10	.	.	.
Lopori		11	32	.	11	47	.	.	.	.	.	.	.
Ndeko		9	7	.	81	2	.	.	.	.	.	.	.
Rubani		8	10	2	69	10	.	.	.	.	.	.	.
Josie		25	42	.	.	.	8	.	.	.	.	25	.
Genet		35	6	6	35	.	18	.	.	.	.	.	.
Tuli	chimpanzee (Twycross)	67	8	2	.	6	12	2	.	4	.	.	.
William		22	39	3	.	.	28	.	.	.	8	.	.
Flyn		45	18	9	.	9	18	.	.	.	.	.	.
Tommie		32	63	.	.	5	.	.	.	.	.	.	.
Kibali		**33**	21	42	.	4	.	.	.	.	.	.	.
Lucy		43	57	.	.	.	.	.	.	.	.	.	.
Eva		2	41	.	.	.	56	.	.	2	.	.	.
Kilimi		18	80	.	.	.	.	.	.	1	.	1	.
Edith		28	72	.	.	.	.	.	.	.	.	.	.
Louis	chimpanzee (Edinburgh)	50	14	.	.	.	36	.	.	.	.	.	.
Qafzeh		3	91	.	.	.	6	.	.	.	.	.	.
Paul		25	70	.	.	.	.	.	.	.	.	5	.
Frek		15	85	.	.	.	.	.	.	.	.	1	.
Velu		.	98	.	.	.	.	.	.	.	.	2	.

Appendix F: Supplementary Methodological and Statistical Information for Chapter 6: Communication and Coordination in a Two-Action Task

Appendix F1. Table of the number of sessions administered to each subject in pre-test 2, before they reached minimum passage criteria (13/16 correct critical trials across two consecutive blocks of 8 critical trials each; trials with a 0-second delay were not included in this metric). All subjects received one initial session of pre-test 2 before attempting to meet passage criteria, thus the minimum possible number of sessions is 3.

Subject	Number of Sessions in Pre-Test 2
Eva	3
Edith	3
Louis	3
David	5
Kilimi	5
Lucy	7
Liberius	7
Qafzeh	7
Velu	7
Frek	11

Appendix F2. Details of interruptions and modifications to the experimental procedure as a result of COVID-19 lockdowns.

Testing was interrupted three times due to COVID-19; twice in adherence to lockdown procedures and once due to lack of access to subjects as a result of the research backlog from previous lockdowns. Certain subjects experienced lapses in testing of up to eight months, and thus, the following accommodations were made:

1. If a subject had more than ten remaining trials in the learning phase, or if the subject was due to begin their refresh learning phase (between the test and communication phases), trials were administered as normal. If a subject had fewer than ten learning trials remaining or was due to begin their test or communication phases, 10 trials from their original learning condition were administered. Thus, all subjects received at least 100 learning trials, and all subjects had received at least 10 learning trials within the same period of testing when they received their test and/or communication phases.
2. If the interruption occurred during a subject's test or communication phase, the phase was restarted, and the old trials discarded, on the grounds that learning may have been occurring between trials, which may not have been retained across the lapse in testing. 10 learning trials were administered prior to the restarting of either the test or the communication phase, as above.

The timing of each subject's progress through the experiment, with respect to COVID-19 lockdowns and related delays, is depicted below:

Appendix F2.1 Table depicting the timing of each subject's progress through the experiment, with lapses in testing included. The phase or trials listed for each subject in each time period indicate the starting (S) and final (F) piece of testing completed within that time period. Any phase that was incomplete and restarted in the next period following a delay is indicated with an (x).

Subject		Sep 2019 – Feb 2020	Mar – Sep 2020	Oct – Dec 2020	Jan – Apr 2021	May 2021	June – Sep 2021	Oct – Nov 2021
Velu	S	pre-test 1		10 refresh trials		n/a		n/a
	F	test phase		completed study		n/a		n/a
Eva	S	pre-test 1		10 refresh trials		n/a		n/a
	F	100 learning trials		completed study		n/a		n/a
Louis	S	pre-test 1		33 learning trials		n/a		n/a
	F	67 learning trials		completed study		n/a		n/a
Kilimi	S	pre-test 1		30 learning trials		n/a		n/a
	F	70 learning trials		completed study		n/a		n/a
Lucy	S	pre-test 1	COVID-19 lockdown	10 refresh trials	COVID-19 lockdown	10 refresh trials	Research delays due to COVID-19 lockdowns	n/a
	F	test phase (x)		test phase		completed study		n/a
Edith	S	pre-test 1		55 learning trials		10 refresh trials		n/a
	F	45 learning trials		test phase (x)		completed study		n/a
Frek	S	pre-test 1		block 8, pre-test 2		67 learning trials		n/a
	F	7 blocks pre-test 2		33 learning trials		completed study		n/a
Qafzeh	S	pre-test 1		68 learning trials		10 learning trials		10 refresh trials
	F	32 learning trials		97 learning trials		test phase		completed study
David	S	pre-test 1		74 learning trials		27 learning trials		10 refresh trials
	F	26 learning trials		73 learning trials		test phase		completed study
Liberius	S	pre-test 1		55 learning trials		10 refresh trials		10 refresh trials
	F	45 learning trials		test phase (x)		test phase (x)		completed study

Appendix F3. Table of VIF or GVIF (only models containing at least one 3-level factor) values to assess multicollinearity in each GLMM of this analysis. Multicollinearity was not a concern in any model; all GVIF values were below 2. Multicollinearity was not assessed in the GLMM concerning flip style, because that model included only one fixed factor.

Variable	Flip Frequency (Test Phase)		Communication Frequency (Test Phase)		Communication Frequency (Communication Phase)	
	VIF	*df*	*VIF*	*df*	*GVIF*	*df*
condition	1.0014	1	1.0706	1	1.0079	1
trial number	1.0013	1	1.0455	1	1.0363	1
pre-pull time	n/a	n/a	1.0593	1	1.1216	1
pre-pull comm.	n/a	n/a	1.0608	1	1.0158	1
trial duration	n/a	n/a	n/a	n/a	1.1183	2
any flip	n/a	n/a	1.0267	1	n/a	n/a

Appendix F4. Detailed ethogram for identification and discrimination of communication behaviours; this exact ethogram was provided during training for reliability coding.

Behaviour	Definition
tap	the subject taps or raps their fingers against the table, window, or apparatus from any side, including beneath. Taps may be single or repetitive and should be counted only once if the subject has not removed their fingers from the mesh between taps. Note that a tap or contact between the fingers and the apparatus performed as part of an action to manipulate the apparatus (i.e., pull the paper, peel the blocks from the table, touch the see-saw, or fish for the grape) should not be counted. Note that taps from beneath, which may lift or rattle the table, should be counted.
finger thrust	the subject thrusts the fingers (or single finger) of one hand through the mesh. Thrusts may be single or repetitive and should be counted only once unless the subject completely ceases the action (either by removing the fingers entirely or by leaving the fingers through the mesh passively) and then subsequently begins again.
head nod	the subject moves their head up and down (nodding) or side to side (shaking, i.e., ear moves toward shoulder) repeatedly (at least two movements) with the eyeline directed at E.
pass paper	the subject pushes a strip of paper (either having already pulled the current piece or using one from the floor) back through the mesh either partially or completely. All motions/thrusts/taps associated with this activity should be counted as one event, unless they completely cease the behaviour (1 second elapses between efforts or the subject engages in another behaviour and then returns to this behaviour) and then resume while the paper is still partially in the mesh.
raspberry	the subject produces a lip buzzing/raspberry sound/mouth gesture. This sound/gesture may be single or repeated but should only be counted twice if the behaviour fully ceases before beginning again.
grumble	the subject produces an audible, low-pitched vocalization, akin to a grunt or grumble
whine	the subject produces a high-pitched vocalization akin to a whine or cry (not a scream or call)
hand fling	the subject raises their hand upward, with the palm facing away from E, and produces a flinging gesture toward the shoulder
present mouth	the subject presents their lips/mouth, open or closed, such that at least one lip protrudes through the mesh. Note that the use of the lips, tongue, or teeth in effort to pull the paper or manipulate the apparatus (e.g., the blocks) should not be counted.

Appendix G: Statement of Ethics and Certificates of Ethical Approval

Each of the four experimental studies presented in this thesis were conducted with ethical approval from the University of St. Andrews School of Psychology and Neuroscience Ethics. Each study also received approval from the Budongo Research Unit Scientific Committee and (in Chapter 4 and Chapter 5) the Twycross Zoo Research Committee. Subjects were treated in compliance with ASAB Guidelines for the treatment of animals in behavioural research and teaching at all times, and participation in each experiment was completely voluntary; subjects were never deprived of food, water, enrichment, or access to groupmates during testing. Testing was conducted in consultation with the animal keeper teams at each zoo to ensure that all research procedures were in the best interests of the animals. I adhered to hygiene and safety procedures related to COVID-19 at all times. Copies of the certificates of ethical approval for each study are reproduced below.

Appendix G1. Chapter 2: Proto-Presumptions of Relevance in Chimpanzees

University of St Andrews

School of Psychology & Neuroscience Ethics Committee

4 December 2018

Dear Elizabeth

Thank you for submitting your application which was considered at the Psychology & Neuroscience School Ethics Committee meeting on the 29th November 2018. The following documents have been reviewed:

1. Animal Ethics Form
2. The Budongo Research Unit: General Information (Details on Research Standards, Training, and Expectations)
3. Data Management Plan

Project Title:	Proto Presumptions of Relevance in Chimpanzees		
Researcher's Name:	Elizabeth Warren		
Supervisor:	Professor Josep Call		
Approved on:	30/11/2018	**Approval Expiry:**	30/11/2023

The School of Psychology & Neuroscience Ethics Committee approves this study from an ethical point of view.

Approval is given for five years. Projects, which have not commenced within two years of original approval, must be re-submitted to the School Ethics Committee.

You must inform the School Ethics Committee when the research has been completed. If you are unable to complete your research within the five-year validation period, you will be required to write to the School Ethics Committee to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and an application for ethical amendment Form submitted where appropriate.

Approval is given on the understanding that the *ASAB Guidelines for the treatment of animals in behavioural research and teaching (ANIMAL BEHAVIOUR, 2018, 135, I-X)* are adhered to.

Yours sincerely

Convenor of the School Ethics Committee

Ccs   Professor Josep Call (Supervisor)
        Dr Tamara Lawson (Home Office Liaison Officer)

SEC Convenor, St Mary's Quad, St Andrews, Fife KY16 9JP, Scotland
Email: psyethics@st-andrews.ac.uk Tel: 01334 462071
The University of St Andrews is a charity registered in Scotland: No SC013532

University of St Andrews

School of Psychology & Neuroscience Ethics Committee

18 September 2020

Dear Elizabeth

Thank you for submitting your application which was considered by the Psychology & Neuroscience School Ethics Committee on 5 August and 16 September 2020. The following documents have been reviewed:

1. Animal Ethics Form
2. External Permissions: Budongo Research Unit
3. Living Links Offices Startup Risk Assessment, Version 5.0: 15th June 2020

Project Title:	Mediating Gaze-Following and Double Looks with Ostensive Behaviour		
Researcher:	Elizabeth Warren		
Supervisor:	Professor Josep Call		
Approved on:	18/09/2020	Approval Expiry:	18/09/2025
SEC Approval Code:	192		

The School of Psychology & Neuroscience Ethics Committee approves this study from an ethical point of view.

Approval is given for five years. Projects, which have not commenced within two years of original approval, must be re-submitted to the School Ethics Committee.

You must inform the School Ethics Committee when the research has been completed. If you are unable to complete your research within the five-year validation period, you will be required to write to the School Ethics Committee to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and an application for ethical amendment Form submitted where appropriate.

Approval is given on the understanding that the *ASAB Guidelines for the treatment of animals in behavioural research and teaching (ANIMAL BEHAVIOUR, 2018, 135, I-X)* are adhered to.

Yours sincerely

Convenor of the School Ethics Committee

Ccs   Professor Josep Call
        Home Office Liaison Officer

SEC Convenor, St Mary's Quad, St Andrews, Fife KY16 9JP, Scotland
Email: psyethics@st-andrews.ac.uk Tel: 01334 462071
The University of St Andrews is a charity registered in Scotland: No SC013532

Appendix G3. Chapter 5: The Effect of Emotional Valence within Ostensive Behaviour on Apes' Expectation of Action

University of St Andrews

School of Psychology & Neuroscience Ethics Committee

22 April 2021

Dear Elizabeth

Thank you for submitting your application which was considered at the Psychology & Neuroscience School Ethics Committee meeting on 15th April 2021. The following documents have been reviewed:

1. Animal Ethics Form
2. External Permissions: Twycross Zoo
3. Copy of Twycross Zoo Covid-19 General Risk Assessment

Project Title:	Mediating Expectation of Action with Ostensive Behaviour: "Wait" versus "Invite"		
Researcher:	Elizabeth Warren		
Supervisor:	Professor Josep Call		
Approved on:	15/04/2021	Approval Expiry:	15/04/2026
SEC Approval Code:	207		

The School of Psychology & Neuroscience Ethics Committee approves this study from an ethical point of view.

Approval is given for five years. Projects, which have not commenced within two years of original approval, must be re-submitted to the School Ethics Committee.

You must inform the School Ethics Committee when the research has been completed. If you are unable to complete your research within the five-year validation period, you will be required to write to the School Ethics Committee to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and an application for ethical amendment Form submitted where appropriate.

Approval is given on the understanding that the *ASAB Guidelines for the treatment of animals in behavioural research and teaching (ANIMAL BEHAVIOUR, 2018, 135, I-X)* are adhered to.

Yours sincerely

Convenor of the School Ethics Committee

Ccs   Professor Josep Call
        Dr Tamara Lawson (Home Office Liaison Officer)

SEC Convenor, St Mary's Quad, St Andrews, Fife KY16 9JP, Scotland
Email: psyethics@st-andrews.ac.uk Tel: 01334 462071
The University of St Andrews is a charity registered in Scotland: No SC013532

University of St Andrews

School of Psychology & Neuroscience Ethics Committee

4th September 2019

Dear Elizabeth and Emma

Thank you for submitting your application which was considered by the Psychology & Neuroscience School Ethics Committee on 20th August 2018. The following documents have been reviewed:

1. Animal Ethics Form
2. Apparatus Graphics and Procedure
   To follow:
   External Permission: Budongo Research Unit (BRU)

Project Title:	Communication and Coordination in a Two-Action Task		
Researchers' Names:	Elizabeth Warren, Emma McEwen, Dr Manon Schweinfurth		
Supervisor:	Professor Josep Call		
Approved on:	28/08/2019	Approval Expiry:	28/08/2024

The School of Psychology & Neuroscience Ethics Committee approves this study from an ethical point of view.

Approval is given for five years. Projects, which have not commenced within two years of original approval, must be re-submitted to the School Ethics Committee.

You must inform the School Ethics Committee when the research has been completed. If you are unable to complete your research within the five-year validation period, you will be required to write to the School Ethics Committee to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and an application for ethical amendment Form submitted where appropriate.

Approval is given on the understanding that the *ASAB Guidelines for the treatment of animals in behavioural research and teaching (ANIMAL BEHAVIOUR, 2018, 135, I-X)* are adhered to.

Yours sincerely

Convenor of the School Ethics Committee

Ccs   Professor Josep Call (Supervisor)
       Dr Tamara Lawson (Home Office Liaison Officer)

SEC Convenor, St Mary's Quad, St Andrews, Fife KY16 9JP, Scotland
Email: psyethics@st-andrews.ac.uk Tel: 01334 462071
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