Cooperation and teaching in the context of cumulative culture

Suska Nolte

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“We are, as Wittgenstein (1953) and Vygotsky (1978) saw so clearly, fish in the water of culture”

(Tomasello, 1999, p. 215)

Abstract

Cumulative culture enables humans to shape their niche and to live in extreme environments. To understand the factors enabling cumulative culture, we need to understand which cognitive abilities support it, how they develop through life, and how they evolved. Different hypotheses have been put forward as to which cognitive abilities – namely innovation, imitation, teaching, and cooperation – are most essential for the emergence of cumulative culture. In this dissertation I review evidence for each these abilities and discuss three studies that I conducted to investigate the latter two concepts – teaching, and cooperation. The first study used a tool-exchange paradigm to compare the altruistic and cooperative abilities of our two closest living relatives, chimpanzees and bonobos. Bonobos were more likely to transfer tools to a partner than chimpanzees in both an altruistic and cooperative context. The second study investigated the ability of chimpanzees to teach new skills to an ignorant conspecific. I found no evidence that chimpanzees were able to teach, even with incentives to do so. This is very different to the behaviour of children in the final study. In this study I investigated whether children, between the ages four to seven years, would teach an ignorant partner and whether the strategies employed depended on their age or the potential benefits of successful teaching. Children of all age groups taught their partner and employed a variety of teaching strategies. Children used more iconic gestures and explanations (i.e. information the partner could directly enact) when they would benefit from having a competent partner rather than a partner whose actions did not result in benefits. I discuss the results of these studies in terms of their implication for the debate on the evolution of cumulative culture and will argue that flexible teaching and enhanced altruistic motivation enabled modern humans to outcompete most species with which we share the planet.

I. Chapter 1: General Introduction

A. Cumulative culture

Cultural technologies, such as medical advances and various kinds of materials, tools, and machines enable modern humans to overcome physiological limitations. The human species has not only been able to adapt and inhabit various habitats, but even to live in originally uninhabitable environments. This so-called cultural niche construction was fundamental to our species' huge evolutionary success (Vale, Davis, Lambeth, Schapiro, & Whiten, 2017). On top of directly modifying given environments such as manipulating lakes to build land or vice versa, humans also obviate the risk of an increasing number of illnesses through preventive medicine and can heal even severe bodily damage. Currently, a project called Mars One seeks to start populating another planet, Mars. Thus, instead of being shaped by the niche, in most cases humans can create durable environmental modifications and shape their niche according to their needs (Richerson & Boyd, 2005). Yet, when stripped of all technologies, we as individuals would most likely not survive (Henrich, 2015). This derives from the fact that we use technologies produced through cumulative culture, which involves the "modification, over multiple transmission episodes, of cultural traits (behavioural patterns transmitted through social learning) resulting in an increase in the complexity or efficiency of those traits" (Dean, Vale, Laland, Flynn, & Kendal, 2014). Thus, cumulative cultural technologies cannot be replicated by a single individual as they are invented through iterative cycles of copying and improvement resulting in sophisticated products (Tomasello, Kruger, & Ratner, 1993). If these products are faithfully transmitted the cognitive load to modify specific parts, once a need for it arises, is kept relatively small and can lead to complex designs that a single individual would not have been able to create (Tomasello et al., 1993). Culture itself, sometimes also called traditions, has been defined as "group-typical behavior patterns shared by members of a community that rely on socially learned and transmitted information" (Laland & Hoppitt, 2003, p. 151; a similar definition has been simultaneously proposed by Fragaszy & Perry, 2003). Therefore, the term cumulative culture adds the requirement for such cultural traits to undergo successive modifications over time resulting in a product that could not be reinvented by a single individual. The ability for cumulative culture can lead to an acceleration in discovering new information about the environment as each piece of information could build upon previous ones (Dean et al., 2014).

The quest to understand whether nonhuman species have cultural traditions leapt forwards in the late 90s. Following McGrew's (1992) work that investigated whether chimpanzees show behavioural differences in cracking palm nuts between several research sites, Whiten and colleagues (1999) expanded this approach and recorded various types of chimpanzee behaviour at seven different research sites across Africa. This research team documented a total of 65 different categories of behaviours that were observed in either of the different populations and argued that they represent a "unique record of the inventiveness of wild chimpanzees" (p. 682). Additionally, the authors were able to reveal that chimpanzee communities differed on 39 of these categories and showed varying behavioural patterns across research sites that could not readily be explained by ecological differences. This finding sparked a debate about whether the behaviours could actually be considered cultural traditions given that it was not possible to clarify whether they were socially transmitted or caused by other factors such as genetic or ecological variables that were not considered (Laland & Janik, 2006).

Tits opening milk bottles (Fisher & Hinde, 1949; Hinde & Fisher, 1951) and macaques washing sweet-potatoes (Kawamura, 1954, 1959) are some of the earliest reports of novel behaviours that spread socially. Furthermore, Allen and colleagues (2013) recorded lobtail feeding, which is a specific hunting technique, in humpback whales and were able to analyse how the behaviour spread within a specific population since the first observation in 1980. Hobaiter and colleagues (2014) subsequently showed the same for the emergence and spread of a newly invented tool technique, termed "moss-sponging", in one chimpanzee community at Budongo Forest, Uganda. Individuals of this community started to use moss to produce a sponge with which they gathered water to drink. The research team showed how the behaviour spread and how it was adopted by other individuals of the same group, with a clear influence of the number of observation events on the learning rate by naïve individuals. These studies were of significant importance as they demonstrated that behaviours can in fact spread socially within populations of nonhuman animals, supporting the view that cultural traditions exist not only in humans (Whiten et al., 1999). Nowadays many researchers acknowledge that several nonhuman species exhibit cultural traditions, support coming from avian species (Aplin et al., 2015; Hunt & Gray, 2003), cetaceans (Whitehead & Rendell, 2014), fish (Helfman & Schultz, 1984; Warner, 1988), and different primate species (Huffman, 1996; Perry et al., 2003; van Schaik et al., 2003; Watanabe, Urasopon, & Malaivijitnond, 2007). Nevertheless, so far we do not find strong evidence that any species apart from humans shows cumulative cultural traditions (Tennie, Call, & Tomasello, 2009).

Over the past two years, however, this view has been challenged and researchers observed changes in behaviour that seem to fit the basic criteria of cumulative cultural evolution. Sasaki and Biro (2017) found that homing pigeons showed continued improvement of homing routes when paired with new partners in contrast to pigeons that flew alone or with a fixed partner. New naive partners obtained route information by following the knowledgeable leader but also improved routes by slightly adapting them. Subsequently (i.e. on the next flight generation), these previously naive pigeons were paired with a new naive partner, who again slightly adapted the route information. This resulted in cumulative improvement in terms of efficiency over consecutive flight generations, while the routes of control pigeons remained unchanged. Pairs at the end of generational succession showed the most efficient homing routes compared to control pigeons, and routes were more similar within than between generation chains. The authors therefore concluded that later generations built on knowledge that was transferred across previous generations, which indicates that “collective intelligence can become a cumulative process in animal groups, [and], by satisfying the main criteria for CCE, they also demonstrate the presence of CCE in a non-human species” (Sasaki & Biro, 2017, p. 2). Furthermore, Jesmer and colleagues (2018) proposed that ungulates such as bighorn sheep and moose obtained knowledge about migratory routes through social learning and cultural transmission. The researchers used GPS collars to track the movement of bighorn sheep and moose from several different populations that were newly translocated to novel landscapes. They compared the migratory skill of new populations with that of populations extant for about 200 years. Foraging knowledge and the propensity to migrate increased as the time since translocation increased. According to the authors, ungulates most likely socially learned efficient foraging routes and further improved them through their own experience. Thus, across generations they became increasingly able to optimally exploit their habitats.

Even though both reports are intriguing and valuable to understand cumulative cultural evolution, the examples do differ to those of humans. First, in both reported cases there was an increase in efficiency but not complexity. Migration efficiency can plateau and reach its maximum, which contrasts the open-endedness of increased complexity of, for example, technological skills (Sasaki & Biro, 2017). Finally, the change of efficiency was somewhat slow as in each generation only slight changes were made to the route. For example, Jesmer and colleagues (2018) reported that it took decades for bighorn sheep and moose to learn and culturally transmit how to effectively forage and migrate. In contrast, cumulative culture in humans allows for very fast successive improvements if needed. Thus, the findings might be less a testament of cumulative cultural ability in other species but that similar results can be achieved through collective learning and without underlying complex cognitive abilities. It, however, still questions the clear distinction between cumulative culture and such phenomenons, and further research is needed to clarify in what way they are similar and whether these examples might reveal precursors of cumulative cultural abilities. Interestingly, both cases involve spacial navigation and we might find more species that rely on such collective knowledge transmission and accumulation. It is quite possible that our ancestors also first relied on collective accumulation of spacial knowledge before being able to rely on cumulative improvements of technological skills. The discussed results highlight the importance of considering other domains, in which populations might accumulate knowledge cumulatively, as most research focuses on technological advances such as tool manufacture in different species. Thus, potential domains might be spacial navigation, communication systems, or other foraging strategies.

To understand how cumulative culture evolved, we can look at the necessary underlying cognitive abilities, the ontogeny of such abilities, and whether we find them in our closest living relatives. The latter two approaches help to clarify if the identified cognitive abilities are actually sufficient and crucial to enable cumulative culture. By looking at the ontogeny of such traits, we can pinpoint at what time cumulative cultural abilities arise and which abilities were already in place before this event. Thus, we know which abilities are sufficient and that any capability arising afterwards is not directly needed for the expression of cumulative culture and might just support it later on. By looking at our closest living relatives, the nonhuman great apes, or possibly other species we can verify which of these abilities are crucial. Even though our closest living relatives possess cultural variation across groups of the same species, no evidence has been produced so far that they possess the ability of cumulative culture (Tennie et al., 2009). Therefore, by comparing which of the target abilities are present versus not present in our closest living relatives, we can pinpoint the specific human abilities that are crucial for the expression of cumulative culture instead of culture itself (i.e. cultural variation).

For this review I will start by giving an overview of the different hypotheses that have been put forward as to which cognitive abilities – namely innovation, imitation, teaching, and cooperation – are most relevant for cumulative culture to emerge. Subsequently, I will introduce the specific studies we conducted to further our understanding of some of the aspects that I discuss in this review.

B. Cognitive abilities

1. Innovation

Before new skills or knowledge can be transmitted and successively improved, innovation is essential to create such new strategies (Enquist, Ghirlanda, Jarrick, & Wachtmeister, 2008). Innovation has been defined as "a solution to a novel problem, or a novel solution to an old one" (Kummer & Goodall, 1985, p. 203). Thus, innovative behaviours typically either arise in response to a new stimulus or by adapting already existing behaviours to reach a new goal (i.e. to be beneficial in a new context). In order to find a solution to a novel problem, the individual needs to be able to adapt old strategies to achieve the new goal (Manrique, Völter, & Call, 2013). As a result, the old strategy is transferred to pursue a new problem. In contrast, to find a novel solution to an old problem, the individual needs to be able to inhibit already learned strategies to discover and act on new solutions (Manrique et al., 2013).

Human children are proficient in understanding the function of tools (Casler & Keleman, 2005), choose the appropriate tool to solve a task (Beck, Apperly, Chappell, Guthrie, & Cutting, 2011), effectively copy tool use techniques by observing others (Hopper, Flynn, Wood, & Whiten, 2010), and in turn subsequently transmit that information to observers (Hopper et al., 2010; Flynn & Whiten, 2008). However, surprisingly it seems that young children are not able to innovate completely novel tools by themselves (Whalley, Cutting, & Beck, 2017). The ability to independently innovate tools seems to only emerge around the age of eight and after children are already proficient in understanding tool properties and copying the manufacturing process (Beck et al., 2011; Whalley et al., 2017). Whalley and colleagues (2017) reported that using a premade tool seemed to be the driving factor of whether young children could manufacture it themselves afterwards. Given that the children did not have problems with understanding what steps were needed to manufacture the tools themselves, it seemed that independently innovating a solution was the most difficult part. Nevertheless, McGuigan, Burdett, Burgess, Dean, Lucas, Vale, and Whiten (2017) showed that children as young as three to four years were able to adapt strategies to solve tasks and improve preexisting tools. Thus, innovative skills seem to be present but not if novel objects need to be invented from scratch. For cumulative culture to arise, however, it is not essential that only novel solutions occur but can also involve a successive improvement of existing strategies. This could explain why we find cumulative cultural abilities in children (McGuigan et al., 2017; Tennie, Walter, Gampe, Carpenter, & Tomasello, 2014) even before they are able to independently innovate novel solutions. It is conceivable that, in humans, the most important aspect for children is to learn population specific conventions and the general physicality of their environment by interacting with it and copying others. Once they become proficient in understanding physical laws, their accumulated repertoire of knowledge might be sufficient to innovate novel solutions by themselves that could then spread in their population.

Several factors, such as an individual's level of curiosity (neophilia), playfulness, and boldness, influence the likelihood that an individual will interact with novel objects (Kuczaj, 2017). Moreover, functional fixedness (i.e. the "inability to use an existing behavior or strategy in a new way"; Kuczaj, 2017, p. 631) and conservatism negatively influence whether an animal will find alternative strategies to solve a given problem (Kuczaj, 2017). Finally, an increased group size has been proposed to buffer against inter-individual variance (Derex, Beugin, Godelle, & Raymond, 2013). I will continue to consider these aspects and their relation to innovation.

Curious individuals tend to be more likely to investigate novel aspects of their environment and thus increase their experience of the environment's affordances (Berlyne, 1950). Birch (1945) showed that gaining experience with stimuli increases the chances that new functional relations are discovered. If such curiosity and perception of affordances is coupled with the ability to reason about causal relationships, the individual is able to form representations of newly discovered effects and reproduce them to reach a desired goal (Call, 2013). According to Mettke-Hofmann (2007), the context influences whether an individual will react neophilically or neophobically to a new stimulus. While some species are curious facing novel food items but are neophobic to novel objects, others show the reverse pattern. This in turn influences where we could expect innovations to arise as they should occur where a given species is found to be most neophilic (Mettke-Hofmann, 2007). Along the same lines, playful and bold individuals will be more likely to gain experience and discover new effects by interacting in a more varied and non-fearful way with the environment, thereby increasing the chances to randomly discover new causal relationships (Kuczaj, 2017).

Nevertheless, while interacting with the environment's stimuli is beneficial for discovering new affordances, gaining experience might also hinder the likelihood that innovative behaviours arise when an individual becomes fixed on its initially discovered function (Manrique et al., 2013). Functional fixedness is the "inability to use an existing behavior or strategy in a new way" (Kuczaj, 2017, p. 631). Thus, gaining experience with objects might increase the likelihood that an individual adapts old strategies to achieve a new goal, but decrease the likelihood that novel solutions are found to achieve an old goal. One proposed reason of why chimpanzees do not show cumulative culture is that they become fixed on or are conservative with regard to old strategies used to solve problems and therefore fail to innovate and cumulatively adapt skills (Hrubesch, Preuschoft, & Schaik, 2009; Marshall-Pescini & Whiten, 2008). Manrique, Völter, and Call (2013) suggested that it might be cognitively more challenging when new solutions have to be found to existing problems because the motor pattern that was learned has to be inhibited. This in turn would make an animal less likely to copy or invent alternative strategies even when those are more efficient. Nevertheless, the researchers showed experimentally that chimpanzees and bonobos are able to switch between solutions for a task that they were familiar with. Both species innovated new solutions to reach the same goal once the old solution became obsolete, showing that they were able to inhibit previously learned solutions and flexibly innovate new ones. It seems that in chimpanzees innovations are most likely produced out of necessity and only when established strategies fail to fulfil the goal (Brosnan & Hopper, 2014). Caldwell and Millen (2010) argued that conservatism might arise when conditions are risky and the pay-off is less predictable. In their study, the researchers asked participants to build a tower as tall as possible. Over consecutive overlapping “generations” the tower was modified and its height was increased showing the capacity for cumulative improvement. However, when the participants were told that the height will be measured after the tower is tested for its durability, the number of modifications was smaller in comparison to when they were told that the height will be measured after 5 minutes upon completion. Given that the environment of chimpanzees can be quite harsh, it is conceivable that this might be one of the factors as to why they maintain working strategies even if others might be more efficient.

Finally, inter-individual variance in cognitive abilities is enhanced in larger groups, which has been argued to lead to an increased likelihood of innovations to occur by buffering against low performing individuals (Derex et al., 2013). According to Derex, Beugin, Godelle, and Raymond (2013), in larger groups more strategies are generally prevalent possibly due to the fact that as group size increases, it results in an increase in instances in which cultural traits could be observed and copied. Thus, if one observes the behaviour of solitary and group living species that both fulfil the discussed traits above, the chances to find innovative behaviours are increased for the latter merely due to the fact that more individuals might show the behaviour preventing it from being extinguished before it could be recorded.

Taken together, we can expect innovative behaviours to be predominantly observed in larger groups whose individuals tend to be playful and can inhibit prepotent responses, and in response to situations or objects for which the given species shows neophilia or when old solutions fail to work. To search for examples of innovation, social learning, and tool use, Reader and Laland (2002) assessed relevant published articles from several primate journals and gathered 2000 papers covering 57% of known primate species. The authors aimed to classify innovative behaviours without their own subjective interpretation of the recorded behaviours, and therefore only included behaviours that were described as "novel" or "never seen before" by the respective authors themselves. They found 533 instances of innovation across the primate kingdom, with large brain sized primate species showing a higher rate of observed innovation. Yet, even though Reader and Laland (2002) showed that innovations are predominantly found in primate species, to date we do not find records of cumulative culture in any primate species except humans (Tennie et al., 2009). This discrepancy shows that innovation might function as a "cultural catalyst" that increases the complexity and variety of skills within a group, but is not sufficient in itself to bring about cumulative cultural traditions (Dean et al., 2014; Pradhan, Tennie, & van Schaik, 2012). In order for individual innovations to be adopted by other group members and passed down to following generations, other cognitive abilities such as social learning mechanisms need to be in place.

2. Social learning

Social learning is any "learning that is facilitated by observation of, or interaction with, another individual (or its products)" (Hoppitt & Laland, 2013, p. 4). Given that social learning inherently takes place in social contexts, we expect it to occur more in species with opportunities for interactions, in comparison to solitary species that have to rely on asocial learning strategies like trial-and-error learning (Aplin, 2016). Asocial learning can be costly and even risky depending on the situation. Thus, an individual that is able to observe other individuals interacting with a given stimulus is granted the advantage that such interactions can be judged as safe or dangerous without having to interact with the stimulus themselves (Kendal, Coolen, van Bergen, & Laland, 2005). Different social learning mechanisms seem sufficient for acquiring different degrees of skill complexity. Such learning mechanisms have been initially classified as imitation (Thorndike, 1898), stimulus/local enhancement (Spence, 1937; Thorpe, 1956), observational conditioning (Mineka, Davidson, Cook, & Keir, 1984), and emulation (Tomasello, 1990). Many more distinctions have been made thereafter (for overview e.g. Hoppitt & Laland, 2008), which led to an increasing difficulty to clearly distinguish concepts and compare results between studies. Call and Carpenter (2002; see also Carpenter & Call, 2002) therefore proposed to focus on what information individuals extract while observing others. They argued that individuals can learn about the actions, results, or goals of the demonstrator. Considering these aspects enables us to know how animals learn and which information, or combination of information, they are able to make use of. For the means of this review I will focus on the main broad categories that seem most relevant for the debate of cultural learning and discuss them in the light of what type of information was extracted by the observing individual.

Stimulus enhancement was coined by Spence (1937) and refers to the "change in the orientation of an observer's behavior toward stimuli associated with previous reinforcement of a demonstrator's behavior" (Beck, 1976, p. 302). Similarly, in *local enhancement* the presence of another individual drives the observer to visit that specific location or interact with stimuli in it (Thorpe, 1956). Thus, in order for stimulus or local enhancement learning to occur, an individual merely attends to the object that the observed individual manipulated, or visits the same location. Neither does the individual need to replicate specific actions performed by the observed individual, nor does it need to understand the result produced or the goal of that individual (Whiten & Ham, 1992). By attending to the manipulated object (e.g. specific type of food) or location (e.g. food site), the individual can then individually learn about its properties using asocial learning mechanisms. Nevertheless, the individual gains an advantage compared to asocial learning as it interacts with stimuli that are supposedly safe and beneficial to use without having to find such items themselves. While stimulus and local enhancement bring about different traditions that might vary across populations of the same species (e.g. which type of food to eat or which tool to use; Fragaszy & Perry, 2003; Laland & Hoppitt, 2003), they do not enable task specific accumulation of modifications as each individual has to learn about the properties anew (Dean et al., 2014). Thus, through stimulus or local enhancement an individual can learn non-cumulative traditions present within a population but will not be able to facilitate iterative changes to existing skills (Matthews, Paukner, & Suomi, 2010).

A further social learning mechanism is *emulation* and was initially used by Tomasello (1990) to describe nonhuman animals' social learning about observed results. This form of social learning encompasses "the individual observing and learning some affordances or changes of state of the inanimate world as a result of the behavior of another animal, and then using what it has learned in devising its own behavioral strategies" (Tomasello, 1996, p. 321). Thus, in contrast to stimulus or local enhancement, individuals learn which object to use and additionally what result can be achieved with it (i.e. which properties the object has). The observer therefore gains the advantage of learning that a certain change or state is possible, which it might not have discovered by itself. Nevertheless, it has to learn which actions are necessary to produce this change or state by itself. Moreover, for reproducing the result it does not need to understand the goal of the demonstrator and might pursue a different goal by reproducing the result.

Whiten and Ham (1992) subsequently coined the term goal-emulation that extends the idea of emulation and incorporates learning about the intended goal of the demonstrator. In contrast to emulation the observer replicates the perceived goal of the demonstrator in addition to replicating the result. To illustrate the difference: When an individual picks up a nut that was cracked open by another individual, it might understand that nuts can crack and might subsequently attempt to crack open other nuts, thereby replicating the observed result. Learning in this scenario would be referred to as emulation. In contrast, when an individual observes the unsuccessful attempts of another individual to crack open nuts, it might still understand the intention (i.e. goal) of the demonstrator without necessarily having seen the result. This might lead the observer to subsequently attempt to crack open nuts as well, thereby replicating the inferred goal. Learning in this scenario would be referred to as goal-emulation. Therefore, in goal-emulation the observer gains the advantage of learning that a certain goal can be attained with the object instead of merely learning about the object's affordances. Distinguishing the two becomes increasingly difficult once the individual observes successful events, and in such cases tests need to carefully distinguish whether the observer attended to the goal in addition to the result. As with emulation, the observer does not learn about the demonstrator's actions. Emulation has been subsequently called end-state emulation to emphasize its distinction to goal-emulation. I will follow others and, henceforth, use the original term "emulation" to encompass both in order to discuss them simultaneously.

Caldwell and colleagues (2009, 2012) showed that end-state emulation is a sufficient social learning mechanism that can achieve transmission and subsequent cumulative modification of products. In two studies, Caldwell and Millen (2009) and Caldwell, Schillinger, Evans, and Hopper (2012) presented adult human participants with a task to build, respectively, a paper airplane and a spaghetti tower. They varied the type of information accessible to the participants and found that they were able to use models or pictures of previous products to recreate and improve them when building an airplane or spaghetti tower of their own. This led to a successive improvement of the products over consecutive "generations" in the experiment. Yet, both experimental tasks involved recreating products for which the steps of the process could be easily inferred from assessing the end product: It was highly process-transparent. This does not fully represent the challenges of human cultural traditions as they are often more complex and process-opaque. Nevertheless, emulation can support high fidelity transmission enabling cumulative improvements when the products and the way to reproduce them remain transparent. Emulation is not sufficient anymore, once these increase in causal opacity or when the product is too complex to replicate by merely assessing the result or goal (Hopper et al., 2010). For such skills, the individual needs to be able to observe each step of the process and faithfully adhere to them in order to reach the desired outcome.

Imitation is broadly defined as "learning the exact motor pattern of a behavior from observing another individual" (Dean et al., 2014). It contrasts emulation in that it is process-oriented instead of product-oriented learning. Thus, through imitation an individual can replicate the manufacturing process of a product (i.e. the behavioural strategy to attain a result), thereby overcoming the fact that it would not be possible to recreate these when merely looking at the end-product. The observer therefore gains the advantage of learning to produce results without having to learn the necessary steps individually. Tomasello (1999) proposed that imitation is one of the key factors enabling faithful transmission of observed behaviours and thus lays the foundation for cumulative culture of more complex and opaque traditions. Two distinctions have been made to account for different degrees in how faithful each step is replicated by the observer, namely over-imitation and rational imitation.

The term over-imitation has been put forward to account for the fact that children were found to copy actions with such fidelity that they also re-enacted clearly unnecessary actions performed by the demonstrator (Lyons, Young, & Keil, 2007). Curiously, the three- to five-year-old children that were tested continued to reproduce all observed actions including the causally irrelevant actions even when they were asked to perform the task quickly, which would have prompted the children to omit the causally irrelevant actions. The authors concluded that children might have perceived the entire action sequence as causally relevant given that the demonstrator intentionally executed each of the actions. They argued that automatically encoding all actions intentionally performed by a model allowed children to “rapidly calibrate their causal beliefs about even the most opaque physical systems” (p. 19751), thereby reducing the cognitive load needed to replicate perceived goals. The finding that the likelihood of an observer to over-imitate action sequences increased instead of weakened with age – with adults copying all actions most faithfully – suggests that other processes than perceiving the actions as causally relevant might play a role (McGuigan, Makinson, & Whiten, 2011). Instead, over-imitation might be explained by conforming to perceived social norms and it might thus be seen as an extension of an adaptive ‘conformist bias’ (McGuigan et al., 2011). Social benefits might explain why humans engage in such seemingly maladaptive and energetically disadvantageous behaviours (Nielsen, Simcock, & Jenkins, 2008) and over-imitation could be a powerful and adaptive strategy to enhance cultural transmission (McGuigan et al., 2011).

This notion is supported by the finding that children will stop over-imitating and use more efficient strategies once an observed inefficient action seems to be induced by external restraints (Gergely, Bekkering, & Király, 2002). In 1988, Meltzoff found that 14-months-old infants would copy the odd behaviour of a demonstrator using his head instead of hands to touch a box that subsequently lightened up. Gergely and colleagues (2002) modified Meltzoff's study and presented children with two instead of one model. Both models operated a button with their head as in the initial study. However, the hands of one were free and could have been used to operate the button, while the arms and hands of the other were bound by a cloth. Thus, in the latter case the restrained hands seemingly prompted the model to operate the button with her head, while there was no obvious external explanation in the former case. Even though all children used their hand at some point during the test, 69% of the children that observed the model without restrained hands also imitated the head movement. In contrast, only 21% of children imitated the head movement after they observed the model that had restrained hands. Thus, children incorporated the information whether the observed action was voluntarily performed or induced by external means (i.e. due to a cloth disabling the hands). This phenomenon was termed rational imitation (Gergely et al., 2002) and resembles emulation in that the result but not all actions are replicated. It differs from emulation in that the observer still consciously pays attention to and learns the actions of the model, but decides to use other actions. In contrast, during emulation the observer only learns something about the result and/or goal but not about the actions and does not decide to act differently to what was observed. Differentiating the two social learning mechanisms poses yet another difficulty and studies need to carefully distinguish whether the subject only learned about the results and/or goals (emulation) or additionally learned about the actions but just did not replicate them (rational imitation).

Both over-imitation and rational imitation allow for high fidelity transmission of complex skills, where the latter enables individuals to adapt observed processes to make them more efficient. From an early age on, children seem adept at using different social learning strategies that can support transmission of cumulative traditions. Nielsen (2006) showed that 12-months-old human children would copy observed outcomes rather than imitate the specific strategies if not given a rational reason as to why it is necessary to copy the exact actions for reaching the outcome. As was discussed above, 14-months-old children still tend to behave similarly (Gergely et al., 2002). In contrast, Nielsen (2006) found that 18-month-olds started to imitate the model's behaviour independent of whether a rational reason was given and by 24 months children mainly used imitation to solve the task. These results support the aforementioned notion that with increasing age, humans tend to replicate observed actions more and more faithfully. Furthermore, already at 14 months, children start to selectively imitate actions performed by an in-group member speaking their native language versus an out-group member speaking a foreign language (Buttelmann, Zmyj, Daum, & Carpenter, 2013). This corroborates the importance of social factors motivating instead of cognitive ability underlying imitation and suggests that the ability for cultural learning arises early in human ontogeny.

To understand what kind of social information chimpanzees use, Price, Lambeth, Schapiro, and Whiten (2009) presented chimpanzees with the task to combine two tools to rake in a reward, and manipulated the degree of information provided in how to build the tool. The researchers showed that chimpanzees were significantly more skilful at building the tool when given the opportunity to observe a conspecific perform the full procedure instead of either observing the conspecific use the already combined tool to rake in a reward or when receiving no demonstration at all. While some chimpanzees still learned how to build the tool only from observing a conspecific use the combined tool, chimpanzees still benefitted the most from observing the entire process. The researchers therefore concluded that "similarly complex tool manufacture in free-ranging chimpanzees is unlikely to be blocked by cognitive deficits in social transmission" (p. 3380). Furthermore, Horner and Whiten (2005) found that chimpanzees re-enacted observed actions when causal information about the properties of the task were lacking and the result could only be reached by closely reproducing the observed actions. Nevertheless, chimpanzees did not over-imitate and only re-enacted the causally relevant actions upon receiving all causally relevant information and observing which actions in the sequence were unnecessary. Similarly, Buttelmann, Carpenter, Call, and Tomasello (2007) replicated the aforementioned study by Gergely and colleagues (2002) and used their design to test chimpanzees that were raised by humans. Akin to human children, these chimpanzees also used their hands to operate the apparatus significantly more often after they saw a human demonstrator use an unusual body part (e.g. his feet) while his hands were occupied in comparison to not occupied. Thus, again chimpanzees used imitation when no reason was apparent as to why the demonstrator used his feet, and emulation (or rational imitation) when the hands of the demonstrator were occupied (Buttelmann et al., 2007).

Thus far, only in a few studies chimpanzees might have imitated specific action sequences (Buttelmann et al., 2007; Hopper et al., 2007; Horner & Whiten, 2005) and more studies are needed to confirm the generalizability of such findings. We currently do not know whether chimpanzees generally pay attention to entire action sequences but rationally imitate in most studies, or whether they predominantly rely on emulation and mostly do not pay attention to actions. Nevertheless, it seems that chimpanzees can in some situations use imitation to solve tasks. Only a few researchers made an effort to include the other great ape species (e.g. Call & Tomasello, 1994; Clay & Tennie, 2017; Stoinski, Wrate, Ure, & Whiten, 2001), and more such studies are needed to broaden our understanding of the origins of complex social learning mechanisms.

To sum up, social learning mechanisms support the transmission of innovative behaviours and enable populations to adapt to changes in the environment more rapidly than without such learning mechanisms in place (Aplin, 2016). While imitation supports high-fidelity transmission of opaque traditions, emulation seems a sufficient learning mechanism that can achieve cumulative culture as it supports transmission of process transparent traditions (Caldwell & Millen, 2009; Caldwell et al., 2012). Even though it has been shown that chimpanzees are able to emulate observed actions (Call, Carpenter, & Tomasello, 2005; Hopper, Lambeth, Schapiro, & Whiten, 2008) and some findings point to the notion that they might be able to imitate (Buttelmann et al., 2007; Hopper et al., 2007; Horner & Whiten, 2005), we currently do not find cumulative cultural ability in chimpanzees (Dean, Kendal, Schapiro, Thierry, & Laland, 2012; Tennie et al., 2009). Other factors might need to be in place in order for cumulative culture to arise. Teaching is one of such factors as it grants the observer to better understand the important steps needed to reach the end-state. Thus, in case the observed individual actively matches its behaviour depending on the observer's skill level, learning of increasingly complex or process opaque behaviours might be enhanced.

3. Teaching

While emulation and imitation support the acquisition of cultural traits, these mechanisms alone are only sufficient to a point to which the observing individuals are able to encode or invent the necessary steps by themselves. Once skills increase in complexity or opaqueness, such as building complex designs or following rituals, merely observing another individual can become insufficient. Thus, teaching - "actively facilitating learning in others" (Hoppitt et al., 2008) - becomes a necessary mechanism. Teaching enables the observer to learn each step in a more effective manner as it channels the learner's conclusions (Kline, 2015). While innovation and social learning needed to be part of the repertoire of the observer, teaching requires the active involvement of the observed individual. That means even if the observer would be able to copy with high fidelity, and innovatively adapt acquired skills, cumulative culture could not arise in case the observed individual is not able or willing to teach once skills become too complex to grasp by merely observing. Different definitions of teaching have been put forward, which I will review next.

The *culture-based* approach proposes no direct operational definition but conceives teaching as the formal, unidirectional, and explicit form of instruction found in schools of Western societies (Lancy, 2016). It is therefore more an "activity or state rather than a discrete behaviour or action" (Kline, 2017, p. 206). Lancy (2016) argues that teaching arose due to cultural changes in WEIRD (Western, Educated, Industrialized, Rich, Democratic) societies and is not the result of evolutionary forces. According to the culture-based approach, for an event to be considered as teaching the instructor and pupil, respectively, need to intend and identify the activity as such (Gaskins & Paradise, 2010). In contrast, instances, in which the focus of the activity is completing a task instead of instructing even if instructing is part of the activity, are considered as informal guided learning (Gaskins & Paradise, 2010). The responsibility to learn is here on part of the participating pupil instead of on the teacher as in formal teaching (Mead, 1970). Thus, as stated by Mead (1970) a shift occurred in Western societies where learning is installed by the teacher and where pupils might not even agree to need it. According to the culture-based view, explicit verbal instructions play a major role in formal teaching, but are mostly absent in non-Western societies (Lancy & Grove, 2010). Even though in examples discussed by Lancy and Grove (2010) adults modified the position of the children's hand during learning episodes, such instances were not considered as teaching as there was little verbal instruction. It is clear that such a restricted view on teaching will not fulfil the purpose of finding the relevant factors favouring the evolution of teaching, but rather illustrate differences in style instead of ability.

In comparison to the culture-based approach, the *mentalistic* approach proposes to define teaching as any "behavior with the intent to facilitate learning in another" (Pearson, 1989, p. 63). Moreover, instead of focusing on the specific style of transmitting knowledge, this approach seeks to identify the underlying cognitive abilities enabling teaching. According to the mentalistic view of teaching, the teacher needs to understand when and what knowledge is lacking (Strauss, Ziv, & Stein, 2002). Kruger & Tomasello (1996) proposed that a theory of mind is necessary in order to understand that another individual is ignorant of certain skills or parts of a skill and to match the task to the level of the observer. Thus, the teacher needs to identify through theory of mind the zone of proximal development of the trainee, which is the "distance between the actual developmental level as determined by independent problem solving and the level of potential development as determined through problem solving under adult guidance or in collaboration with more capable peers" (Vygotsky, 1978, p. 86). Moreover, the teacher needs to be able to plan ahead into the future in order to understand that the teaching actions now will result in an anticipated outcome on part of the trainee later (Vale, Flynn, & Kendal, 2012). Finally, in addition to such foresight and assessing the knowledge state of the trainee, the teacher needs to intend to teach as is specified by the operational definition used by the mentalistic approach. Advocates of this approach concluded that teaching and its underlying abilities are unique in the human taxon (Premack & Premack, 2018; Strauss et al., 2002; Tomasello et al., 1993). Yet, given that mental processes such as an intent to teach or a representation of the other's level of skill while teaching are difficult to identify, the mentalistic approach is hard if not impossible to implement when assessing the overt behaviour of nonhuman species. Nevertheless, once a behaviour has been identified as teaching, we can return to the mentalistic approach to understand which cognitive capacities are needed to support the specific teaching behaviour.

In order to identify specific behaviours as teaching without having to take into account the underlying cognitive mechanisms, Caro and Hauser (1992) proposed the *functionalistic* approach. The authors argue that by adopting a mentalistic view, different forms of teaching might be overlooked thereby restricting our understanding of this phenomenon. They state that "guided instruction without these [mentalistic] prerequisites could still be favored by natural selection" (Caro & Hauser, 1992). To identify teaching through assessing overt behaviour, the authors put forward three criteria that have to be fulfilled in order to classify an observed behaviour as teaching: (1) "An individual actor A can be said to teach if it modifies its behaviour only in the presence of the naïve observer", which entails encouraging, punishing, providing opportunities to learn, or demonstrating the naïve individual; (2) the behaviour has to come "at some cost or at least without obtaining an immediate benefit for itself"; (3) a naïve individual should "acquire knowledge, or learn a skill earlier in life or more rapidly or efficiently than it might otherwise do, or would not learn at all" (p. 153). As each of these criteria is directly observable, the functionalistic approach is more applicable when classifying behaviours throughout the animal kingdom given that it would not be possible to assess their true mental states during such activities. Indeed, applying this approach showed that some species perform behaviours that do fulfil the criteria stated above. There is strong evidence that we find the ability to teach in the following three species: Tandem-running ants (Franks & Richardson, 2006), meerkats (Thornton & McAuliffe, 2006), and pied babblers (Raihani & Ridley, 2008). Some less solid evidence comes from various other species such as felines (Caro, 1980, 1995), bees (Aguilar & Briceño, 2002; Riley, Greggers, Smith, Reynolds, & Menzel, 2005), atlantic spotted dolphins (Bender, Herzing, & Bjorklund, 2009), killer whales (Guinet & Bouvier, 1995; Lopez & Lopez, 1985), and hens (Nicol & Pope, 1996).

In early 2006, Franks and Richardson reported that they observed a behaviour fulfilling all three criteria of Caro and Hauser's (1992) definition of teaching. Upon encountering a new food site, tandem-running ants (*Temnothorax albipennis*) start to guide a naïve nest mate to this new site. During such tandem-running events, the knowledgeable individual starts moving towards the new location while throughout the journey the naïve individual frequently taps onto the leader's legs or abdomen with its antennae. As soon as the naïve ant stops tapping, the leader immediately pauses and only continues once the naïve ant starts tapping again, thereby allowing the follower to investigate landmarks on the route. Through this system, the leader is modifying its behaviour based on the speed and ability of the follower, ensuring that the follower will learn the route to the food site. When travelling back followers tend to take more direct paths back and show that they did indeed learn the route and not specific path taken. Subsequently, they can become leaders as well. In some instances, knowledgeable ants will carry instead of guide naïve nest mates. This way, both ants will arrive at the location faster but no learning on part of the naïve individual occurs.

Shortly after such teaching in tandem-running ants was described, Thornton and McAuliffe (2006) reported another intriguing behaviour found in meerkats (*Suricata suricatta*). Since meerkats are cooperative breeders, pups are reared by all group members that often are kin to each other as the dominant male and female produce 80% of the offspring (Thornton & McAuliffe, 2006). Meerkats live in harsh environments, in which hunting prey such as scorpions can become quite risky. Thornton and McAuliffe (2006) observed that, while growing up, pups are provided disabled prey (e.g. scorpions with its sting removed) by group members. Even though providing live prey can become costly in case it escapes or injures the pups, this creates opportunities for the pups to learn how to hunt and kill prey effectively. Helpers are guided by the call type of the pups that indicate the pup's age, and will disable prey correspondingly. Thus, youngest pups are provided with dead or highly disabled prey while with increasing age prey is provided increasingly intact. Moreover, pups are monitored by the helpers during handling the prey and, in case they do not engage with the prey, helpers will start to draw attention to it by nudging it until the pup engages – especially if the prey type is rare. Again, this behaviour and the duration of monitoring decreases with increasing age of the pup. Overall, this shows that helpers not only adjusted their behaviour to the age of the pups but also to their immediate behaviour.

The third species that was found to fulfil all functional criteria of teaching is the pied babbler (*Turdoides bicolor*). In earlier work, Raihani and Ridley (2007) found that parents and helpers of this cooperatively breeding bird species emitted a specific type of purr call to divert fledglings from dangerous situations and to guide them through their territory. The authors then found that adults emitted the same purr shortly before and while feeding the young nestlings even though these are still immobile and would not be able to approach (Raihani & Ridley, 2008). Moreover, the call did not seem to increase efficiency of feeding the nestlings. Instead, the nestlings came to associate the specific call with food delivery and once they were mobile started to approach their parents or helpers upon hearing the call. Raihani & Ridley (2008) consider the adult pied babblers' behaviour as a form of active conditioning that is later used to move their fledglings around as needed.

Some researchers have argued that the second criterion of Caro and Hauser's (1992) definition is contradicting as individuals are ultimately always benefitting from teaching (Kline, 2017). According to evolutionary theory, teaching will only arise if there are long-term benefits even if the actor gains no immediate benefit from it (Thornton & Raihani, 2010). Moreover, if the second criterion is applied in a strict sense, formal teachers are not considered to be teaching due to the fact that they are paid for their activity and, thus, gain a benefit from it. Nevertheless, if this criterion were to be dropped, the definition would become too inclusive. Let's consider an example where one animal acts in an aggressive manner towards another group member each time they encounter. The first criterion of Caro and Hauser's (1992) definition would be fulfilled as the actor changes its behaviour in the presence of the group member. The second criterion would also be fulfilled as the group member will eventually start to avoid the actor and, thus, learn something through the behaviour of the actor (i.e. that it is unpleasant to approach the actor). Such an example occurs in most group-living species and can be easily transformed to fit any other interactive instance. This shows that without the second criterion, most species would be considered to teach one way or another. However, if we apply the second criterion such instances would not be included as the actor in our example gains the immediate and primary benefit of the group member leaving. Kline's (2017) criticism is nevertheless still valid in that the definition does not specify how immediate a benefit can result for the action to still be considered teaching. Thornton and Raihani (2010) state that in addition to the second criterion, no other alternative primary function of the given teaching instance should be apparent. Applying this additional criterion will help to distinguish teaching from behaviours such as parental provisioning. In such an example, the three criteria would often be fulfilled (i.e. (1) parents adapt their behaviour in the presence of young; (2) giving food is costly and no immediate benefit results except for reproductive fitness, which is the case in most teaching instances; (3) the young might learn something about which food to consume). However, the primary function is providing nutrition and not that the offspring learns which food to consume. Thus, evidence is required that the specific behaviour was selected to facilitate learning (Hoppitt et al., 2008). In each of the aforementioned examples of teaching (i.e. tandem-running ants, meerkats, pied babblers), the respective researchers were able to show that up until now no alternative function than promoting learning could be related to the observed behaviour.

According to Thornton and Raihani (2010), Caro and Hauser's (1992) criteria are useful to identify whether an observed behaviour can be considered as teaching, but "it does not provide a conceptual basis for understanding what teaching is and where best to look for it" (p. 298). The authors propose several characteristics that can guide researchers in where to expect teaching behaviour. According to them, teaching will most likely occur between closely related individuals or between parents and their offspring. For example, eusocial insects or cooperative breeding species, especially where helpers are closely related kin, pose good candidates for teaching to arise because the inclusive fitness outweighs incurring the costs of teaching. Cooperative breeding creates a system, in which it is beneficial to invest even in unrelated offspring due to indirect reciprocity (Bergmüller, Johnstone, Russell, & Bshary, 2007). Moreover, teaching becomes less costly as the task is shared with other group members (Thornton, 2008). Indeed, each of the four species, which so far have been found to teach, fit this hypothesis: Tandem-running ants are eusocial insects, while meerkats, pied babblers, and humans live in cooperative breeding societies that care for related and unrelated kin. Nevertheless, there are many more species that breed cooperatively but are not found to teach and being closely related, as are parents and their offspring, is certainly not sufficient to engage in teaching.

Thornton and Raihani (2010) further suggest that environmental factors greatly influence whether the benefits of engaging in teaching outweigh the costs, which can be energetic costs or lost resources. They integrate findings from their studies on meerkats and pied babblers (see above) and report that individuals of both species adjust their behaviour depending on the costs involved. Meerkats are sensitive to the size of their prey and tend to kill larger prey more frequently than smaller prey. They also monitor pups more intently after they received live instead of dead and large instead of small prey (Thornton, 2008). This is in line with the idea that teaching can become quite costly once pups lose prey and meerkats seem to act accordingly. Similarly, in pied babblers subordinates but not dominants reduce the amount of purr calls given while feeding nestlings when food is scarce during dry periods. Thornton and Raihani (2010) relate this finding to the poorer foraging skills of subordinates due to their younger age, which might cause subordinates to be reluctant to engage in purr calls while feeding nestlings when the conditions are harsher. Finally, Möglich (1978) reports that in six out of seven tested species of the genus *Leptothorax*, tandem-running always occurred at the start of migrating to a new nest site and decreased over time. The reverse pattern was true for instances of knowledgeable individuals carrying nest mates. Never were tandem-runs observed at the end of migrating and, on average, seemed to be terminated after the first third of the moving process was completed and enough knowledgeable individuals were recruited to complete the remaining two thirds. The authors hypothesize that the condition of the old nest site and thus urgency to move might be one factor influencing how many ants were observed to tandem-run. These findings show that environmental conditions can negatively or positively influence the occurrence of teaching and should be taken into consideration by researchers trying to find teaching in other species.

Furthermore, Thornton and Raihani (2010) state that the observing individual needs to have the capacity of social learning that corresponds to the level of teaching provided, which again can guide researchers in where to expect what kind, if any, of teaching to occur. Finally, Thornton and Raihani (2010) propose that teaching is expected where individual learning is costly or might not occur at all. On the other hand, in species where observing other group members or parents might be sufficient to individually acquire skills, we would not expect teaching to arise as it would be redundant or not in balance with the costs incurred. For example, group-hunting provides ample experience through observation and would render it inefficient to teach how to hunt (Thornton & Raihani, 2010). In comparison, species that hunt individually would benefit from active demonstrations (Thornton & Raihani, 2010). Indeed, the lack of teaching found in chimpanzees has been related to the fact that, while growing up, young chimpanzees have ample opportunities to observe their mothers and other group members during their activities, such as using tools (Tennie et al., 2009).

As was discussed earlier, chimpanzees are well able to socially learn new skills through observation. Up to date, only Boesch (1991) and Musgrave, Morgan, Lonsdorf, Mundry, and Sanz (2016) report that chimpanzees teach. In 1991, Boesch found anecdotal evidence of two chimpanzee mothers at Tai forest, Ivory coast, as to actively teach their respective child how to crack nuts. One example involves a mother that, after her child struggled to use a hammer, slowly rotated that hammer into the correct position before starting to crack a nut herself with her child watching. In a second example, a mother positioned a nut into the correct position on the anvil before her child continued to pound it with the hammer. Musgrave and colleagues (2016) reported that tool transfers between chimpanzee mothers and their infants can be considered as a form of teaching which sticks are usable. Up to date, it remains unknown whether these instances occurred with the intent to teach and whether other chimpanzee populations might show similar behaviours. I will consider the different hypothesis of why we currently do not have clear evidence that chimpanzees might teach in more depth in chapter three.

In humans, the use of language during teaching most likely strongly impacted the efficiency of teaching and enabled the transmission of more complex skills. Morgan and colleagues (2015) aimed to reconstruct how the knowledge to manufacture Oldowan tools might have been transmitted within communities and how, in turn, different forms of communication might have been selected for because humans relied on tool use. The researchers presented participants with stones that they could knap to produce Oldowan tool-like flakes, and varied which information was available to the new participant. Thus, participants could either learn the technique through reverse engineering (i.e. only the manufactured flakes were given), imitation/emulation (participants could observe a tutor during the manufacturing process), basic teaching (tutors not only demonstrated how to manufacture the tools but also slowed down their movements, shifted their body to allow for better visibility, and corrected errors of the participants by moulding their grasp on the hammer- or core-stone), gestural teaching (tutors showed the correct motions through gestures), verbal teaching (tutors could verbally explain the procedure). The main finding was that any teaching resulted in a better skill acquisition by participants than reverse engineering or imitation/emulation, and that flake quality only improved through gestural or verbal teaching. Only when the tutor was allowed to use language could participants produce the largest number of viable flakes per minute in comparison to reverse engineering and imitation/emulation. Moreover, even though there was no statistical difference between gestural and verbal teaching, the latter consistently resulted in a better performance across all measured assessments. Given that there was a continuous improvement in the transmission of knapping skills from reverse engineering to verbal communication, the research team concluded that a gene-culture co-evolution would be the most plausible explanation of how human technology evolved. Fitness benefits most likely resulted for individuals that were able to use more complex forms of communication during teaching, in turn allowing for better tool manufacture and subsequently again resulted in fitness benefits for renewed improvement in communication. Thus, Morgan and colleagues (2015) attribute the rise of Oldowan technology with the rise of language and argue that the co-evolutionary dynamic resulted in a selection favouring abilities with which information could be transmitted on a more and more abstract level. Gärdenfors and Högberg (2017) extended this idea and proposed that during the rise of Acheulean technology even more complex levels of communication evolved, including communication of concepts and explaining the relationship between these. According to the authors, these capacities built on the existing teaching abilities that evolved during the Oldowan period and gave way to the eventual evolution of modern language capabilities and societies.

In summary: Teaching should involve the modification of the actor's behaviour in the presence of a naïve partner, no immediate benefits should result from the action, evidence is needed that it does not fulfil any other primary function than facilitating learning, and the naïve individual needs to acquire a behaviour that it would not have acquired at all (or with more effort) in case no teaching would have occurred. Improvement has to be made in defining how immediate benefits can be gained for an action to still be considered as teaching. We should expect teaching to occur between individuals that are either closely related or gain a net-benefit from it due to their social structure. Moreover, environmental influences, social learning capability, and individual social learning opportunity are factors that can narrow down where it might be beneficial to search for teaching. More studies on a variety of species are needed to verify and understand which of the proposed factors directly influences the expression and favours the evolution of teaching. It is striking that solid evidence thus far has been found in an insect, bird, and mammal species, and it is yet unknown which cognitive capacities are underlying these instances of teaching. Applying the mentalistic approach might be helpful to inspire future studies in this domain.

Notably, each of the reported behaviours is observed in one specific context and not transferred to teach or reward different skills or responses. This suggests that teaching behaviour in these examples is an adaptive response to the environment and does not necessarily involve complex cognition. Meerkats for example will start providing intact prey to very young pups when calls of older pups are played back in an experimental setting (Thornton & McAuliffe, 2006). Assessing the age and thus corresponding ability of their pups through calls, instead of reflecting on individual ability, is on average a safe and simultaneously less demanding strategy. This shows that teaching can possibly arise without complex underlying cognition as long as it is tailored to one specific and somewhat stable context. Some degree of flexibility exists as individuals of the respective species respond to energetic costs involved and are sensitive to external factors such as prey size, food abundance, and amount of knowledgeable nest mates present. Yet, this stands in contrast to how humans teach, which occurs in various contexts and through different modalities, pointing to a “generalized capacity for teaching” (Hoppitt & Laland, 2013). This generalized capacity to teach has been proposed to have coevolved with the capacity for cumulative culture (Fogarty, Strimling, & Laland, 2011). It is yet unknown whether differences between the observed behaviours of humans and nonhuman species are of degree or kind and which specific factors might have enabled the evolution for a general ability to teach. I will further reflect upon human teaching in chapter four.

4. Cooperation

Our societies are built on cooperation between unrelated individuals, nowadays bridging continents. We use an arbitrary piece of paper (i.e. money) to regulate and somewhat enforce cooperative acts, and denote how much each act is worth in comparison to other acts. Every individual that is part of this system and contributes to it with their specific type of labour will receive a specific amount of paper and can in return exchange it for the products or labour of other individuals. Such a system creates opportunities to specialize and focus on one type of labour and to trade one's products for the products of others without having to memorize deeds done and received. It creates a somewhat fair exchange of deeds on a large scale across the globe and even between individuals that one has never interacted with. It goes without saying that this system is unfair in many respects as power can guide how much worth is arbitrarily attributed to which type of labour, and the same labour can have a different monetary value depending on external factors such as in which country it is done. Nevertheless, such a scale of cooperation connecting populations across the globe is undocumented in any animal other than the human.

The term cooperation has been defined as actions that are beneficial to both the actor and the recipient (Staub, 1978). In order for a cooperative act to occur, both individuals need to invest something into reaching a mutual goal and consequently both gain a benefit from it. In comparison, an action is considered to be altruistic if it only results in a benefit for the recipient but not for the actor (Eisenberg & Miller, 1987). Behaviours are only considered altruistic if they were selected to induce a benefit in the recipient, which rules out actions with an alternative primary function that still result in incidental benefits as by-products (West, El Mouden, & Gardner, 2011). Some definitions also include the notion that for an action to be considered altruistic the donor needs to incur a cost (Trivers, 1971; Wilson, 1975). The magnitude of the cost that has to be paid differs between definitions and can range from having to incur a cost that is detrimental to the donor's direct fitness (Trivers, 1971) to having to invest some energy in the process of helping (Warneken & Tomasello, 2006). Observations of seemingly altruistic acts posed a puzzle for the traditional Darwinian view as genes should not be selected for if they lead individuals to perform actions that result in no benefit for the actor but only for another individual. However, Hamilton (1964) put forward the term ‘inclusive fitness’ to explain why cooperative or altruistic strategies can be favoured by natural selection. Inclusive fitness denotes the sum of direct (i.e. passing on copies of one’s own genes through producing offspring) and indirect fitness (i.e. passing on copies of one’s own genes through supporting offspring of related individuals). This explains why genes, which support such systems as found in eusocial insects, continued to be selected: Workers are more closely related to their sisters than they would be to their own offspring and, thus, gain a greater inclusive fitness by supporting sisters instead of producing offspring. Similarly, closely related but non-eusocial individuals gain a greater inclusive fitness if they produce own offspring and simultaneously help to support the offspring of their close kin. This process has been termed ‘kin selection’ and was defined as “the evolution of characteristics which favour the survival of close relatives of the affected individual, by processes which do not require any discontinuities in population breeding structure”(Smith, 1964, p. 1145).

Genes that lead to an investment even into unrelated offspring or cooperate with unrelated individuals can also arise through natural selection if costs are returned at some point in the future (Nowak, 2006). The mechanisms that could support such social systems are direct and indirect reciprocity and I will consider both in more detail now.

Trivers (1971) put forward the notion of direct reciprocity to explain how altruism between unrelated individuals could be favoured by natural selection. According to the mechanism of direct reciprocity, individuals should be more likely to help others that have helped them before and punish defectors that did not reciprocate received favours (Trivers, 1971). Such a system ensures some protection against cheaters and enables cooperative and altruistic genes to be beneficial in the long run and, thus, be selected for. To understand how the described system might arise, Axelrod (1984) compared different strategies of how someone might respond to the actions of a partner. He showed that a computer program that responded to partners in a ‘tit-for-tat’ manner would achieve the highest number of points. The tit-for-tat strategy starts out by cooperating with the partner and is then mirroring the choices made by the partner (i.e. cooperate or defect). The success of this system has been attributed to the fact that it starts with being cooperative, retaliates upon defection, is also forgiving (i.e. cooperates again after another cooperative event), and is easy to understand as the responses are very clear (Axelrod & Dion, 1988). However, tit-for-tat does not allow for mistakes as this might result in a subsequent circle of retaliation, which would result in non-cooperative systems under natural sometimes erroneous conditions (Nowak, 2006). Therefore, Nowak and Sigmund (1993) applied the learning-rule ‘win-stay, lose-shift’, in which players base their next response on whether their prior response led to a negative or positive outcome for themselves. In case both players cooperate, both win and stay with their response. In case player A defects while player B cooperates, player A will win and stay with the response but player B will lose and switch the response, in this case to defection. Thus, on the next round both individuals will defect and lose, which will make both individuals switch their response on the next trial and cooperate again. This model can more readily explain how altruistic behaviours among unrelated individuals in a population might have evolved as it accounts for the fact that accidental defections can occur in a natural environment and prevents iterations of retaliation once an individual defects. It is also called the Pavlov strategy because response switching can occur without reflecting on the options and merely due to avoiding a response that led to a negative outcome before (Nowak & Sigmund, 1993). The same strategy can be found in non-cooperative games such as Rock-Paper-Scissors and points to a more general response pattern (Wang, Xu, & Zhou, 2015).

Direct reciprocity can only be beneficial if the same individuals repeatedly interact with one another over time and can establish a stable relationship. This might pose several difficulties: Individuals have to remember with whom they last interacted with and in what manner; they will need to be able to help on a constant basis or else risk defection themselves; and individuals might die or leave the group, which would bear a great cost for establishing dyadic cooperative relationships (Nowak, 2006). Indirect reciprocity, or third party altruism, can reduce the impact of these difficulties in that it generates a more dynamic cooperative system among numerous individuals of a population (Alexander, 1987). Yet, third-party interactions are much more difficult to track. To illustrate, specific interactions such as “individual A donated food to individual B, individual B defected when engaging with individual C, but individual C donated food to individual D” would have to be mapped and remembered. Instead of remembering who owes a deed to whom that could in return be directed towards the bystander, this individual could base the decision with whom to cooperate on observing the reaction of the group member. The bystander should then decide to invest into the group member that was helpful, regardless to whom. Thus, reputation instead of a memory of all encounters guides decisions with whom to cooperate and thus facilitates indirect reciprocal systems (Nowak & Sigmund, 2005). The influence of reputation via bystander observation and its effect on the likelihood to engage with the observed individuals has been shown in human adults (Wedekind & Milinski, 2000), preverbal infants (Hamlin, Wynn, & Bloom, 2007), chimpanzees and orangutans (Hermann, Keupp, Hare, Vaish, & Tomasello, 2013), dogs (Marshall-Pescini, Passalacqua, Ferrario, Valsecchi, & Prato-Previde, 2011), and coral reef fish (Pinto, Oates, Grutter, & Bshary, 2011).

Bshary and Schäffer (2002), for example, showed that cleaner fish (*Labroides dimidiatus*) have the choice to either cooperate and eat the ectoparasites on their clients' skin or defect and bite off pieces from the more preferred mucus. The latter is hurtful to clients, which leads them to chase away and subsequently avoid this particular cleaner fish when they next visit cleaning stations (Bshary & Schäffer, 2002). To prevent interactions even before a cleaner fish can cheat, clients register whether a particular cleaner fish is cooperating with or defecting their current client and avoid those that they observed to defect (Pinto et al., 2011). Conversely, cleaner fish show higher levels of cooperation when bystander fish are present (Pinto et al., 2011) or after they were punished and avoided (Bshary & Grutter, 2005). They also use altruistic acts such as positive tactile stimulation (giving them a back rub) when the client is small, cheat least when the client is a predator, and cheat most when the client is a non-predator and resident fish as the options to switch and visit other cleaner fish are minimized for such residents (Salwiczek et al., 2012). Bshary (2002) also found that using tactile stimulation for one client was followed by cheating the next more often than expected by chance. Cleaner fish therefore show great sensitivity to their audience and incorporate different factors such as whether clients can easily leave and visit other cleaner fish.

In humans, the influence of reputation via bystander observation and its effect on the likelihood to engage with the observed agents could be recorded from an early age on. Already six-months-old human infants are sensitive to whether an observed agent is helpful or harmful towards another agent and change their own approach correspondingly (Hamlin et al., 2007). The infants were shown video clips in which an agent either (1) helped another agent by pushing it up a hill, (2) harmed that agent by pushing it down the hill, or (3) behaved neutral and moved up or down the hill without interacting with the agent in need. Subsequently, the infants were given the choice to reach for objects that represented the three different agents. When given the choice between the helpful and harmful agent, all 6-month-old children reached for the object representing the helpful agent. When given a choice between the helpful and neutral agent infants again showed a preference for the helpful agent, but when given a choice between the harmful and neutral agent they preferred the neutral agent. Thus, these preverbal infants showed a clear sensitivity to the valence of observed interactions, both with regard to negative and positive interactions. Such an early sensitivity shows the importance of reputation effects influencing human interactions.

As group size increases it will become increasingly difficult to preserve an accurate representation of all group members' reputation (Nowak & Sigmund, 1998). Individuals of a population will not be able to observe every interaction between other group members, leading to different representations between different individuals (Nowak & Sigmund, 1998). In humans, gossip can function as a way to assess and update the reputation of other individuals in addition to observing interactions themselves (Nowak, 2006). Therefore, in big groups it can buffer against diminished chances of directly observing all interactions.

Sommerfeld, Krambeck, Semmann, and Milinski (2007) showed that information about group members was successfully transmitted via gossip in an experimental setting, and that it facilitated indirect reciprocity. In this experiment, multiple participants interacted with another over the course of three rounds. Anonymity was ensured throughout the entire experiment and each interaction only lasted one round, thus expectation of direct reciprocity should not influence the results. First, participants were given the chance to write a short statement about another person for whom they received direct and true information on their level of altruism (i.e. donating money to another participant during a past round). The participants who wrote the statement were aware that it will be the only information with which the next partner of this person could judge whether to be altruistic him- or herself. The authors found that participants accurately incorporated the information they received and wrote increasingly positive reports the more often the person in question had donated on previous trials. Subsequently, these reports were given to another participant before this new participant had to interact with the person in question. The authors found that new participants were more likely to donate money to the person in question upon reading positive than upon reading negative descriptions about him or her. Thus, the gossip directly influenced whether participants would donate money to the person even though they themselves did not interact with him or her before. Following this round, participants interacted with a second partner for whom they now received direct and true information about his or her responses during the prior second round. Additionally, the authors manipulated which type of gossip the participant received about the partner's choices during the initial first round. This information did not reflect the actual choices but was ranging from extremely negative to extremely positive statements. Sommerfeld and colleagues (2007) found that the manipulated gossip statement strongly affected response rates even though the participants could assess their partner via direct information from their behaviour during the second - more recent - round. If participants received negative gossip they were less likely to donate money to their partner than when they received positive gossip. However, both extreme positive and negative gossip had the least impact on the subsequent choice and the researchers interpreted this finding as people being more questioning of extreme statements after they had actually received direct information about the person in question. Still, Sommerfeld and colleagues (2007) showed that gossip - even in the face of direct information - can influence people's inclination to be altruistic: They punish upon hearing negative gossip and are benevolent upon hearing positive gossip. Given that anonymity was ensured throughout the entire experiment, effects will most likely be even stronger in naturalistic settings in which people put a name to their gossip.

Gossip can be a means to learn and communicate social norms of the respective cultural environment (Noon & Delbridge, 1993). Social norms have been defined as "standards of behaviour that are based on widely shared beliefs how individual group members ought to behave in a given situation" (Fehr & Fischbacher, 2004, p. 185). Norms regulate and somewhat force cooperative exchanges as they formulate clear punishments for defecting individuals, and thereby allow third-party punishment and even legal enforcement (Fehr & Fischbacher, 2004). When an individual is primed towards certain social norms by observing or hearing relevant cues (e.g. seeing another person litter), these norms will be consciously or unconsciously recalled and are more likely to be enacted thereafter.

Schmidt, Rakoczy, and Tomasello (2012) showed that children as young as three years are aware of social norms and enforce them selectively for ingroup members only. Krupka and Weber (2009) further tested whether directly observing the behaviour of others or merely being led to think about norms will influence adult participants' willingness to donate money to another participant. Participants were placed in a context where they had to choose between either behaving selfish ("giving $7 to the chooser and $1 to the recipient") or altruistic ("giving $5 to both"). Each participant only played one round with the partner, so neither repetition nor reciprocity could influence the responses. The authors found that there was no difference in whether participants had to reflect upon what others think they should do (direct cuing) or what they think others might have done (indirect cuing). Both direct and indirect cuing led participants to act more altruistic than when no cuing occurred. Moreover, the number of altruistic choices also increased when participants received direct information that others had behaved altruistically. Thus, it did not make a difference whether participants were cued to think about social norms directly or indirectly or whether they received actual information that other participants behaved altruistic. Surprisingly, even upon observing that the majority had defected, participants still behaved more altruistic than when they did not receive any information. This shows that even negative examples can be enough to facilitate an unconscious or conscious recalling of social norms, which subsequently influences one's own choices. Given that in this experiment no consequences resulted from defection, no strategical considerations were required, and participants acted less altruistically when no information or cuing was given. The authors concluded that the observed increase in altruistic behaviours was due to a direct influence of social norms.

Thus, in combination with audience effects, reputation, and third-party punishment, social norms create strong forces to behave altruistically towards individuals that are unrelated. Due to the fact that all members of a group are influenced by these forces and thus more likely to behave altruistically, direct and indirect reciprocity in turn increase each individual's inclusive fitness. This enables a group as a whole to become fitter than groups that lack the described social dynamics. Therefore, groups that are able to establish cooperation between individuals through altered social dynamics will consequently gain a greater overall fitness benefit and outcompete groups and other species without such cooperative interactions (Nowak, 2006).

While gossip cannot be found outside the human taxon as it is supported by advanced language skills, social norms could be enforced without language and through ostracism or physical punishment. Nevertheless, to this date we lack clear evidence that one of our closest living relatives, the chimpanzee, follows social norms and enacts them through third-party punishment (Schlingloff & Moore, 2017). Only a few studies so far have pointed into the direction that individual chimpanzees might perceive and follow social norms of their group (van Leeuwen, Cronin, & Haun, 2014; Luncz, Wittig, & Boesch, 2015). For example, Luncz, Wittig, and Boesch (2015) discovered that females who immigrated between communities in the Taï National Park (Côte d'Ivoire, West Africa) started to apply the tools predominantly used in their new group instead of continuing to use the tools they used while residing in their old group. The researchers controlled for ecological differences and argued that the finding points towards conformity tendencies of the new females. Furthermore, such behaviour could be advantageous to the females as it might help them integrate into their new group more smoothly (Luncz et al., 2015). However, we are still lacking evidence that this is actually the case and that females perceive the usage of different tools as social norms that they want to abide by. Instead, they might be driven to use the new tools due to alternative reasons such as salience and stimulus enhancement. To understand if conformity might be a beneficial strategy to avoid ostracism, another group of researchers directly tested whether chimpanzees would punish nonconforming individuals upon observing them stealing the food of a conspecific (Riedl, Jensen, Call, & Tomasello, 2012). However, the researchers found that even though chimpanzees retaliated when the conspecific stole their own food, they would not do the same when the conspecific stole another individual's food. Thus, we currently do not have evidence that chimpanzees use third-party punishment to inflict costs upon group members that did not behave prosocially. Furthermore, even though chimpanzees use observations about conspecifics to guide their choice with whom to cooperate (Herrmann et al., 2013) it does not seem that they in return try to be perceived as cooperative by their group members (Engelmann, Herrmann, & Tomasello, 2012). Yet, this conclusion is based on one study and we are additionally lacking information on our other closest living relative, the bonobo. More studies are needed to confirm the lack of third-party punishment and reputation management in closely related species. I will discuss differences between bonobos' and chimpanzees' general cooperative tendencies in chapter 2.

To conclude, reciprocal altruism between unrelated individuals that is regulated via social norms and gossip most likely led to the large-scale cooperation found in modern humans. Even though the scale of the cooperative system put forward in the introductory example (i.e. using money to regulate exchanges across the globe) is impressive, we find similar mechanisms that regulate cooperation between unrelated individuals within societies where members are mostly connected to individuals of their own population (Hill et al., 2011). In addition to arising early in ontogeny, this fact points to a social structure that is unique and universal in humans. Regulated altruistic and cooperative exchanges allow for more frequent and possibly more tolerant interactions, which in turn increase the chance for observing and socially learning skills or rare innovations (Hill et al., 2011). Moreover, teaching has been classified as a form of altruism as the teacher provides knowledge or induces a new behaviour that is immediately or ultimately beneficial for the trainee (Fogarty et al., 2011; Tennie et al., 2009). In such social structures, the costs of complex social learning mechanisms become outweighed by the benefits and result in an accumulation of more complex cultural traditions (Hill et al., 2011). Thus, the authors propose that in humans, compared to other animals capable of social learning, cumulative culture might have been made possible through the development of a "metagroup social structure" (Hill et al., 2011, p. 1286).

C. Aims

I reviewed the main cognitive abilities – innovation, emulation/imitation, teaching, and cooperation – that have been proposed to be most relevant for cumulative culture to emerge. As I discussed, innovation and emulation/imitation by themselves do not seem sufficient to enable cumulative cultural evolution. Nevertheless, they are important aspects that support it. The purpose of this dissertation is to investigate the two remaining aspects – teaching and cooperation – in more detail. The main goals are to understand 1) how motivational aspects govern whether chimpanzees and bonobos act prosocially towards a conspecific, 2) whether chimpanzees teach, and 3) how motivational aspects influence whether children teach and which strategies they employ. Subsequently, I will discuss the results in light of cumulative culture and which abilities might be crucial for its evolution. Given that designing and discussing the studies was a collaborative process, I find it important to give credit and will use the term "we" when discussing the individual studies.

In chapter 2, I will introduce two experiments that we conducted to directly compare the inclination of chimpanzees and bonobos to transfer tools to a conspecific in need. The set-up of both experiments remained the same and we only varied whether the actor gained a direct benefit from transferring a tool or whether this was done altruistically. Thus, we incorporated a cooperative task, during which both conspecifics gained rewards through cooperation, and an instrumental helping task, during which the helper did not gain a benefit by helping. Moreover, we assessed whether the apes can tailor their help according to the specific needs of the conspecific and differentiate between their own and the other's needs. This study gives a unique opportunity to directly assess species' differences and understand which motivation and cognitive complexity underlies cooperative instances in our closest living relatives.

In chapter 3, I will introduce two experiments with which we investigated chimpanzees' ability and motivation to teach an action sequence, composed of two motions, to a conspecific. We used motion trackers to record the exact movements performed by both individuals. With this technology, we were able to analyse even subtle changes in behaviour, such as slowing down or separating both motions. As in the previous study, we varied whether the teacher benefitted from transmitting knowledge or not, while keeping the set-up constant between experiments. This study gives insight into whether chimpanzees are able to understand that the partner lacks certain knowledge and whether they try to transmit information to their partner by demonstrating the correct movements. Thus far, researchers only assessed clearly visible behaviour to understand whether chimpanzees might teach. Using motion trackers allows to assess more subtle cues and we can additionally understand which motivation is driving knowledge provision.

In chapter 4, I will introduce two experiments for which we adapted the procedure of the previous study to assess what means children use to teach one another. In order to understand how teaching might have evolved it is important to assess the developmental trajectory of teaching strategies. The most evolutionarily ancient abilities might also provide the foundation during development for more sophisticated later-evolving strategies. We therefore tested 3.5- to 7.5-year-old children. The age difference within each pair was maximally six months to control for adjustments in teaching strategies due to the age of the partner. We measured whether they used their own apparatus to demonstrate the relevant actions, whether children used gestures to show them, or whether they used different types of verbal directives. Again, as in the previous study we incorporated two experiments, one in which children gained a direct benefit from transmitting information and the second in which they did not. This allowed us to understand how the teaching strategies changed depending on whether children gained a benefit through teaching.

II. Chapter 2: Helping & Cooperation

A. Introduction

As was illustrated in chapter 1, cooperation is a central part of human nature and arises early in ontogeny. It is still unclear to what extent our closest living primate relatives share these tendencies or whether the ability to cooperate flexibly with other individuals has evolved in the human lineage. Comparing human cooperative abilities to those of our closest living relatives enables us to estimate which factors were necessary to facilitate the evolution of cooperative traits. Therefore, I will review what we know of chimpanzees' cooperative tendencies and subsequently discuss the bonobo, our other closest living relative. As was discussed earlier, Staub (1978) defined cooperation as actions that are beneficial to both the actor and the recipient.

In the wild, chimpanzees have been observed to cooperate in various contexts. The most well-known examples of cooperation include meat sharing after hunting (Mitani & Watts, 2001), agonistic support (Watts, 2002), reciprocal grooming (Watts, 2002), reciprocal trade across different commodities (e.g. grooming for support or meat; Mitani, 2006), formation of short- and long-term coalitions to outperform rival males within their group (Duffy, Wrangham, & Silk, 2007), and coalition formation during patrolling the territory and fighting against other males (Watts & Mitani, 2001). Additionally, it is debated whether male chimpanzees actively cooperate and coordinate their actions during hunting colobus monkeys (Boesch & Boesch, 1989). Boesch and Boesch (1989) argue that chimpanzees of the Tai forest (Ivory Coast) coordinate and take on different roles during such hunting. This finding is limited to one population only and it is still not clear whether chimpanzees indeed coordinate their actions during hunting or whether opportunistic strategies are at the core of the seemingly cooperative behaviours (Gilby et al., 2015). The same holds true for each of the other cooperative behaviours that have been reported and it is unknown to what degree the individual understands the role of the partner. Researchers tried to elucidate this question by conducting experimental studies.

The first observation and experiment that investigated cooperative behaviour in captive chimpanzees date back to the early 1900s. After Köhler's observations (1925/1927) of possible cooperation of chimpanzees jointly relocating a heavy cage to climb it and reach food, Crawford (1937) conducted the first controlled experiment that investigated whether pairs of chimpanzees were able to cooperate by each pulling a rope in order to move a box baited with food to within their reach. Only through simultaneously pulling at both ends were the apes able to move the heavy box. The chimpanzees did not spontaneously cooperate with one another and started to cooperate only after the experimenter actively trained the apes to pull in the box. Furthermore, given that the task could possibly be solved by randomly pulling on the ropes, no thorough understanding of the role of the partner was required. After these pioneering studies and only from the 90s onwards, renewed interest in the domain of cooperative tendencies in great apes arose and more experiments were conducted (Povinelli, Nelson, & Boysen, 1992; Chalmeau, 1994; Chalmeau & Gallo, 1996).

To date, we know that chimpanzees can cooperate with one another in various experimental settings. For example, Hirata and Fuwa (2007) elegantly modified Crawford's (1937) original apparatus to assess whether chimpanzees indeed understand that they have to cooperate with one another. In their study, chimpanzees had to haul in a platform placed out of immediate reach by jointly pulling at a rope. Food was located on either end of the platform, which could only be reached once the apes hauled in the platform. The main adaptation to Crawford's task was that the rope unthreaded without moving the platform in case only one chimpanzee pulled at the rope. Therefore, the chimpanzees had to understand that the presence of the other individual is necessary to complete the task. This design is nowadays called 'loose string paradigm' and has been widely used to study cooperation in different species (e.g. Marshall-Pescini, Schwarz, Kostelnik, Virányi, & Range, 2017; Plotnik, Lair, Suphachoksahakun, & Waal, 2011; Schmelz, Duguid, Bohn, & Völter, 2017; Seed, Clayton, & Emery, 2008). Using this paradigm, it was possible to show that chimpanzees in fact understood the role of their partner (Melis, Hare, & Tomasello, 2006a). Chimpanzees opened a door of a neighbouring cage to allow the partner to enter the room and work on the task collaboratively. They were also sensitive to the performance of their partner and, when given the chance to choose between two previous partners, chose the individual with whom they previously cooperated more successfully (Melis et al., 2006a).

Nevertheless, these behaviours immediately extinguished if the partner could monopolize the food located on the tray and no benefits resulted for the subject (Melis, Hare, & Tomasello, 2006b). While humans prefer to solve tasks collaboratively instead of individually, the same does not hold true for chimpanzees. They chose to not involve a conspecific when given the choice between operating an apparatus by themselves or doing it jointly with a conspecific (Rekers, Haun, & Tomasello, 2011). These results call into question the nature of the underlying motivations of cooperative behaviours observed in chimpanzees. Are they performed because of altruistic motivations, hence intended to benefit the partner, or merely arise out of self-interest? To answer this question, researchers have conducted different studies, in which subjects did not directly benefit from their actions as was the case in the latter scenarios.

Such studies can be classified into two broad categories. The first is the 'prosocial choice paradigm' that places the subject in a situation, in which it is necessary to choose one of two different options. Most commonly, the subject is given the choice between an option that provides a reward to both the recipient and the actor (prosocial option), and between an option that only provides a reward to the actor (selfish option). From the viewpoint of the actor both options are identical since during both the actor will receive the same amount of food. The only difference is whether the conspecific is simultaneously rewarded. Thus, it is possible to investigate whether the subject is sensitive to the welfare of a conspecific and acts accordingly without incurring any costs. The second type of design that is frequently used to study altruistic responses in primates is termed the 'instrumental helping paradigm'. This task investigates whether subjects would provide active help to a conspecific that cannot achieve a goal by herself. The more specific term used here is 'instrumental helping', also called 'targeted helping', which has been defined as "help and care based on a cognitive appreciation of the other's specific need or situation" (de Waal, 2008, p. 285). The mixed findings of these studies means that we cannot draw definite conclusions as to whether chimpanzees share altruistic motivations with humans (e.g. Amici, Visalberghi, & Call, 2014; Chalmeau, 1994; Horner, Carter, Suchak, & de Waal, 2011; Liebal, Vaish, Haun, & Tomasello, 2014; D. Povinelli, Nelson, & Boysen, 1992; Warneken, Hare, Melis, Hanus, & Tomasello, 2007; Yamamoto, Humle, & Tanaka, 2009). I will continue to discuss different reasons of why such disparate findings might have occurred, and which factors might support or hinder the expression of prosocial behaviour in chimpanzees.

One proposed reason is that the context in which chimpanzees were placed influenced their responses (Yamamoto & Takimoto, 2012). When placed in scenarios classified as ‘prosocial choice paradigm’, chimpanzees picked randomly between both options when a conspecific was present and when the cage was empty (Silk et al., 2005; Jensen, Hare, Call, & Tomasello, 2006; Vonk et al., 2008; Amici et al., 2014, but see Horner et al., 2011). These results led some researchers to conclude that chimpanzees are generally indifferent to their partners’ welfare (Silk et al., 2005; Jensen et al., 2006; Vonk et al., 2008). However, others propose that such ‘prosocial choice paradigms’ might inherently be too difficult to understand as even children sometimes failed to understand the task’s contingencies (Tan, Kwetuenda, & Hare, 2015). For example, while children acted prosocially when this came at a cost to them, they did not when it was cost-free (Burkart & Rueth, 2013). The researchers suggested that children might not have understood the task’s contingencies, which supports the notion that slight differences in design can lead to outcomes of seemingly unprosocial individuals (Burkart & Rueth, 2013). Therefore, the ‘prosocial choice paradigm’ in itself might be too difficult to understand and results in too many false negatives. This is supported by the fact that, overall, the ‘instrumental helping paradigm’ led to more positive results and chimpanzees indeed seem willing to help another conspecific achieve direct goals without benefiting from such help. For example, Warneken and colleagues (2007) found that chimpanzees released a peg that unlocked a door, enabling a conspecific to enter an adjacent room and consume food there. Similarly, chimpanzees provided access to rewards by releasing a peg that held a baited apparatus out of reach from a conspecific (Melis et al., 2011). Finally, Yamamoto and colleagues (Yamamoto et al., 2009; Yamamoto, Humle, & Tanaka, 2012) reported that chimpanzees transferred objects to a conspecific which allowed her to rake in food that was placed out of reach (but see Liebal et al., 2014). Such results seem to suggest that chimpanzees actually do behave prosocial towards conspecifics, and behaviours observed in wild populations could have such underlying intentions. Therefore, differences between the two paradigms might stem from methodological artefacts: The contingencies of the 'prosocial choice paradigm' might be inherently too opaque, while the salience of the conspecific's goals in 'instrumental helping paradigms' might facilitate task understanding (Yamamoto & Takimoto, 2012).

Another potential factor that could influence whether chimpanzees act prosocially is whether the partner draws attention to herself and the task by making noise or begging (Melis et al., 2011). This could further facilitate understanding as the goals are made more salient (Melis et al., 2011). The absence of prosocial behaviour might therefore be due to the absence of signalling behaviour (or to the external constraints hindering the conspecific from requesting in an effective manner) and not the paradigm itself. Indeed, in several studies that obtained positive results, the partners signaled their need. For example, they stretched their arm into the subject's cage in order to reach for the needed object or shook a chain connected to the apparatus (e.g. Melis et al., 2011; Yamamoto et al., 2009, 2012).

Tennie, Jensen, and Call (2016), however, proposed that such signalling behaviours could elicit response rates not because it facilitates understanding but acts as stimulus enhancement. The authors adapted the design used by Melis and colleagues (2011) and introduced an additional condition, in which pulling the peg hindered instead of granted access to the apparatus and its rewards. Thus, they tried to determine whether prosocial or spiteful intentions might underlie peg releases and predicted to find no difference between both conditions. Instead, they predicted that signalling behaviours will lead to peg releases in both conditions. Indeed, they found that manipulation rates were the same irrespective of the outcome for the partner. The authors suggested that such actions were therefore most likely done because of stimulus enhancement and not because of either prosocial or spiteful underlying motivations. These results call into question the interpretation of previous results, in which chimpanzees had to manipulate an object to help the partner (e.g. Melis et al., 2011; Warneken et al., 2007).

Though bonobos and chimpanzees are similarly closely related to humans, chimpanzees are often used as the representative of the great ape family and our closest living relative, neglecting species differences. This renders the conclusions drawn about the evolution of human prosocial abilities biased towards the behaviour of a single species. There is little evidence that bonobos hunt together in the wild or go on collective boundary patrols, but like chimpanzees they console group members and allogroom (Clay & Waal, 2013; Takeshi Furuichi, 2011; Sakamaki, 2013; Surbeck & Hohmann, 2008). Similar to chimpanzees, bonobos form coalitions and support each other during agonistic fights, however, not between males but between females (Tokuyama & Furuichi, 2016). Given that in both species females are the dispersing sex and migrate to other groups after adolescence, coalition formation occurs irrespective of kin-relationship in bonobos (Tokuyama & Furuichi, 2016). Bonobos are less aggressive towards group members and outside groups, which is mainly driven by the females in the group that eventually engage in sexual contact upon encounter, easing tension between and within groups (Takeshi Furuichi, 2011). Comparing the brains of the two species showed that bonobos have more gray matter in the right anterior insula, the amygdala, and a pathway linking the amygdala and the ventral medial prefrontal cortex (Rilling et al., 2012). In humans, these areas are part of the visceral brain centres and involved in heightened autonomic reactivity to emotional stimuli (Ormel et al., 2013), supporting socio-emotional processing and possibly empathy through emotional contagion and interoceptive abilities (Critchley, Eccles, & Garfinkel, 2013). Herrmann and colleagues (2010) found that in comparison to chimpanzees bonobos performed better on tasks related to theory of mind abilities, possibly reflecting the differences found in brain areas. Clay and colleagues (2016) showed that bonobos are sensitive to whether social expectations during aggressive conflicts are violated. Screams emitted by victims of aggression varied depending on whether the aggression was unexpected or could be socially predicted (e.g. during resource competition). Even though more research is needed to understand the motivation to emit such distinct screams, bonobos seem to possess social expectations based on the situation they are in and what events preceded it. Using eye-tracking, Kano, Hirata, and Call (2015) revealed that bonobos looked at the face and eyes of conspecifics longer than chimpanzees did. This finding further supports the idea that bonobos might be more motivated and possibly skilled than chimpanzees to attend to social cues. Taken together, bonobos seem more adept at processing socially relevant stimuli, however, we do not know whether this heightened awareness and cognitive ability translates into more altruistic responses.

So far only a handful of experimental studies directly compared the overt behaviour of the two species. Most studies focused on either species, making it difficult to assess if differences might be due to methodological rather than species differences. Hare and colleagues (Hare, Melis, Woods, Hastings, & Wrangham, 2007) found that bonobos cooperated significantly more than chimpanzees. The researchers used the loose string task explained above and varied the distance between the food-trays placed on the platform. The closer the trays, the less likely chimpanzees were to cooperate and pull at the ropes. Bonobos on the other hand continued to cooperate irrespective of the distance. Hare and colleagues (2007) argued that bonobos' greater level of social tolerance might have influenced this result and enabled them to sit close to each other and feed together, whereas chimpanzees could not. Similarly, bonobos transferred more tokens to conspecifics than chimpanzees in a token exchange paradigm (Pelé, Dufour, Thierry, & Call, 2009). In this task, both individuals of a dyad were presented with several tokens of two different types. Both individuals could exchange one of the two token types with the experimenter for food and the target type was the opposite for both conspecifics. Thus, in order to maximize the amount of rewards, the apes had to understand that they could exchange their own useless tokens with the another and thereby increase the amount of valuable tokens for themselves. These two studies suggest that bonobos are more adept at cooperating with one another than chimpanzees. Three additional studies found that neither species acted prosocially towards a conspecific: Neither bonobos nor chimpanzees transferred tools to a partner in need (Liebal et al., 2014), shared food with a conspecific by opening a door into their own cage (Bullinger, Burkart, Melis, & Tomasello, 2013), or chose a prosocial option more often than a selfish one (Amici et al., 2014). Only Jaeggi and colleagues (2010) advocated that chimpanzees are more prosocial than bonobos. In their study, chimpanzees transferred food more tolerantly and proactively to conspecifics than bonobos.

To sum up, the mixed findings with regard to altruistic tendencies of chimpanzees might be either due to the paradigm that the respective researcher used, or influenced by whether partners signalled their need that in turn could facilitate whether subjects understand their partner's goal. Tennie and colleagues (2016), however, showed that the relationship between signalling behaviour and increased prosocial responses might be due to stimulus enhancement instead of facilitated understanding. Even though some results (e.g. Yamamoto et al., 2009, 2012) cannot be explained by mere stimulus enhancement as the objects could not be touched by the recipient, it is important to understand the extent to which such actions are prosocially motivated. Furthermore, past studies that directly compared bonobos and chimpanzees found that bonobos seem more adept at processing socially relevant stimuli and performed better on two studies involving cooperative tasks. However, bonobos were similarly reluctant to behave altruistic towards a conspecific and one study found that chimpanzees shared food more proactively to conspecifics than bonobos. From these few studies it seems that bonobos are better at solving cooperative tasks, while they might be similarly unmotivated to help conspecifics or are even less altruistic than chimpanzees. Such mixed and somewhat contradictory results reveal a need for further experiments that directly compare the two species.

To address these missing pieces of information, we tested both species and directly compared their responses. Moreover, we incorporated two experiments in our study: One in which the target action of the subject possibly resulted in direct benefits for the subject and her partner, and one in which it only resulted in direct benefits for the partner. All other parameters were held constant across both experiments. This gives a unique opportunity to answer two questions while controlling for methodological artefacts. The first is whether bonobos and chimpanzees differ in terms of their ability to solve cooperative tasks and their motivation to behave altruistically. As was already said, the small number of studies that included both species resulted in mixed results especially when comparing results across studies that investigated cooperative and altruistic tendencies. The second question answers how subjects respond to their partner's need when they benefit in comparison to when they do not benefit from helping. Through this we could gauge the motivational aspects underlying prosocial behaviour in our two closest living relatives.

We assessed six chimpanzee and six bonobo dyads and presented them with an instrumental helping task, during which the helper did not gain a benefit by helping, and a cooperative task, during which both conspecifics gained rewards through cooperation. In both tasks one individual ('helper') was given access to tools while the partner ('receiver') could only operate her apparatus and access the rewards upon receiving the correct tool from the helper. The only difference between the two tasks was whether the helper had a direct benefit from transferring a tool or not: In case the helper transferred no or an incorrect tool, the receiver could not operate her side of the apparatus and the rewards remained blocked for both individuals. Comparing these two tasks allowed us not only to understand species differences but also to investigate whether tool transfers were done with a prosocial motivation or merely out of self-interest. Additionally, we examined whether the helper was able to distinguish between her own and the other's needs in order to gauge the cognitive complexity underlying helping and cooperation. Depending on the condition, both conspecifics needed to use the same tool type or different tools. In the latter case, the helper had to perform a self-other distinction and understand that the partner needed a different tool to the one she needed herself. Human children become increasingly able to understand that partners' needs might be diverging from their own only around the age of two years (Zahn-Waxler & Radke-Yarrow, 1990), and to our knowledge this is the first experiment specifically addressing the question of whether nonhuman great apes can demonstrate such a self-other distinction during helping or cooperating.

B. Methods

1. Subjects

We tested six bonobos (5 females and 1 male, M_{age}= 12.08) and six chimpanzees (3 females and 3 males, M_{age}= 17.42) housed at the Wolfgang Köhler Primate Research Center at the Zoo Leipzig, Germany (see Table 2.1). Both species were housed in their respective social group in an indoor enclosure and during summer in an additional outdoor enclosure. At the start of the study, all individuals had lived at the zoo for at least one year, been subjected to a variety of cognitive tests, and were used to the handling procedure during tests. Each ape was mother-reared except for two bonobos and one chimpanzee, which were nursery-reared. We included one mother-daughter pair of each species, though the bonobo offspring (Fimi) was younger than the chimpanzee (Kara; see Table 2.1). We additionally included a pair composed of two male chimpanzees that were maternal siblings. The apes were at no point food or water deprived, and during testing water was provided ad libitum. During data collection of this study, none of the apes was in the testing rooms for longer than 30 minutes on a given testing day.

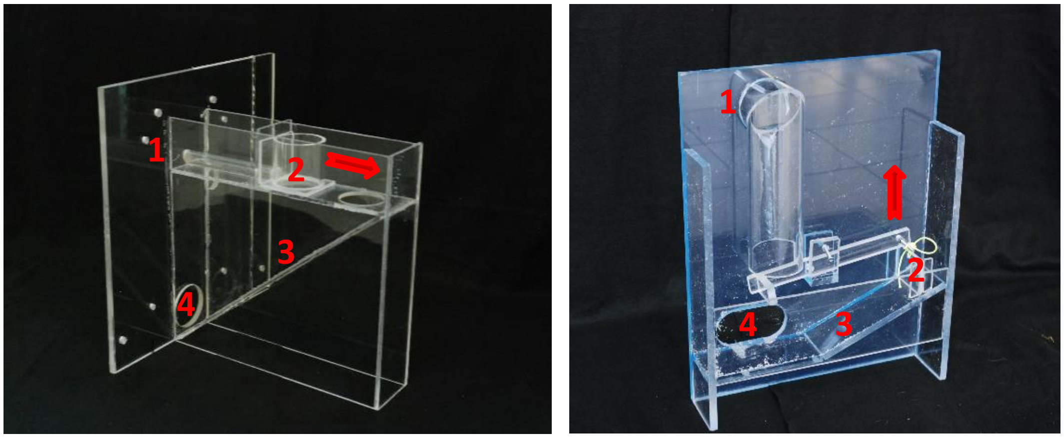
Table 2.1 Details of each subject.

Name	Sex	Species	Age (in years)	Mother	Father	Rearing
Yasa	F	Bonobo	16.7	Diatou	Kakowet II	parent
Fimi	F	Bonobo	5.8	Yasa	Kuno	parent
Gemena	F	Bonobo	8.5	Cheka	Kakowet II	parent
Kuno	M	Bonobo	17.5	Kombote	Maskini	Hand
Lexi	F	Bonobo	14.7	Lorel	Bosondjo	Hand
Luiza	F	Bonobo	9.3	Ulindi	Limbuko	parent
Fraukje	F	Chimp	38.9	Louise	Unknown	Hand
Kara	F	Chimp	9.7	Fraukje	Robert	parent
Kofi	M	Chimp	9.7	Ulla	Robert	parent
Lobo	M	Chimp	10.9	Corrie	Robert	parent
Lome	M	Chimp	13.6	Corrie	Robert	parent
Sandra	F	Chimp	21.7	Riet	Robert	parent

2. Apparatuses

In experiment ‘Helping’, we used two distinct apparatuses that could each be operated by a respective tool. In experiment ‘Cooperation’ we used four apparatuses that were a combination of the original two.

The first apparatus we used in experiment ‘Helping’ (hereafter, ‘apparatus Stick’; see Figure 2.1) could be operated by a wooden stick of 25 cm length and 0.6 cm in diameter. To successfully operate this apparatus, the ape had to insert the stick into a small tube at the top of the apparatus. Subsequently she had to push the stick forward to slide a small container that held the rewards forward. Inserting the stick entirely into the tube moved the container above a hole where the rewards fell onto a slide. This slide led towards the mesh of the ape’s cage (i.e. feeding area), where she could pick up the rewards and consume them. The stick stayed available to the ape throughout the entire session as it was easily retrievable from the apparatus by pulling it out of the tube. The second apparatus in experiment ‘Helping’ (hereafter, ‘apparatus Block’; see Figure 2.1) could be operated by a 3.5 cm wide quadratic block made of solid plastic. For successful operation, the ape had to insert the block into a round hole at the top of the apparatus. Dropping the block through the hole caused a lever to tilt by the block's weight. The lever was connected to a plastic barrier with a string. As the lever tilted the string was pulled upward, thereby pulling the plastic barrier with it and releasing the rewards. The rewards subsequently rolled down the slide and towards the mesh of the ape's cage (i.e. feeding area). As with the stick, the block stayed available throughout the entire session because as soon as the lever was tilted the block slid down and rolled to the mesh.



Apparatus 'Stick'

Apparatus 'Block'

Figure 2.1 Picture of 'apparatus Stick' and 'apparatus Block'. The flat surface was attached to the testing cage and faced the ape. Red numbers indicate the location where the tool needed to be inserted (1), the location of the grapes (2), the slide (3), and the feeding area (4). Red arrows respectively indicate the direction of movement of the container or lever.

In experiment 'Cooperation' we used four distinct apparatuses that were a combination of the two original ones and could be operated by the same tools. These apparatuses were built to form a 90° angle, so that both sides could be attached to the respective mesh of two adjacent cages and operated simultaneously (see Figure 2.2 and 2.5). Instead of using only one tool, the apes now had to use two tools to operate any of the four apparatuses. The general mechanism was the same for each apparatus: Two platforms hindered the rewards from falling down onto a slide. One platform could be released by operating one side of the apparatus and the other platform could be released by operating the other side of the apparatus. In case the left side was operated first, the rewards fell onto the next lower platform and stayed there until the right side was operated as well. In case the right side was operated first, the rewards stayed on the upper left platform but fell down immediately once that platform was released since the lower right platform had already been released. This way, it did not matter which platform was released first and the rewards stayed in place until both sides were operated. After successfully operating both sides, exactly five grapes fell down onto each of two slides and rolled towards the respective mesh of both cages where the corresponding ape could consume them.

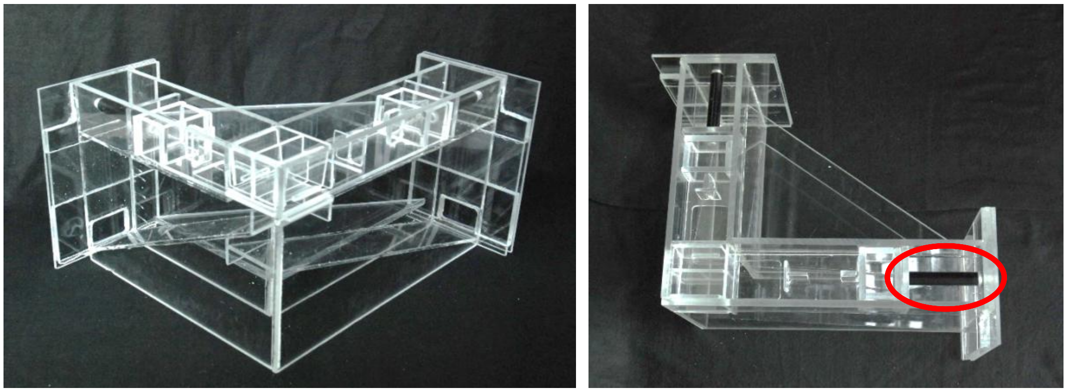
The first apparatus (hereafter, ‘apparatus Stick-Stick’; see Figure 2.2) could be operated by a wooden stick of 25 cm length and 0.6 cm in diameter at both sides of the apparatus. To successfully operate this apparatus, the ape had to insert the stick into a small tube at the top of the apparatus. By pushing the stick forward, the platform was also pushed forward so that the hole in the platform was moved underneath the rewards. The rewards consequently fell onto the next platform, which could be moved by inserting the stick on the other side of the apparatus. At this side, the mechanism was the same. By inserting the stick into the small tube on the other side, the second platform was also pushed forward until the second hole was moved underneath the rewards. Therefore, now the rewards could fall through both holes and onto the respective slides. The stick stayed available to the ape throughout the entire session as it was easily retrievable from the apparatus by pulling it out of either tube.

The second apparatus (hereafter, ‘apparatus Block-Block’; see Figure 2.2) could be operated by a 3.5 cm wide quadratic block made out of solid plastic at both sides of the apparatus. In order to successfully operate this apparatus, the ape had to insert the block into a quadratic opening at the top of the apparatus. By dropping the block through the opening, the block fell onto a tilting device that was tipped over by the block’s weight. A string, which was attached to both a weight and the platform, was held in place by the tilting device. Once the tilting device tipped over the string was released and the weight fell down, thereby pulling the platform away from the rewards. Thus, the rewards that were placed on top of the platform consequently fell onto the next platform, which could be moved by inserting the block on the other side of the apparatus. At this side, the mechanism was the same. By inserting the block into the quadratic opening on the other side, the second tilting device tipped over, released the string, and allowed the weight to fall down thereby pulling away the platform. Now, the rewards could fall down onto the respective slides. As with the stick, the block stayed available throughout the entire session because as soon as the respective tilting device was tipped over the block slid down and rolled to the mesh.

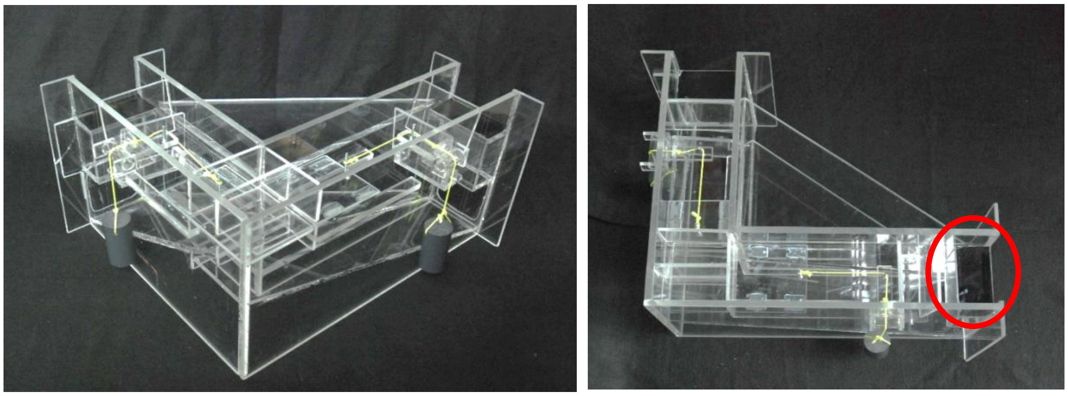
The third and fourth apparatuses had the same combination of mechanisms but the sides were swapped. Thus, the third apparatus (hereafter, ‘apparatus Block-Stick’; see Figure 2.2) could be operated by a block on the left side and a stick on the right side of the apparatus. Conversely, the fourth apparatus (hereafter, ‘apparatus Stick-Block’) could be operated by a stick on the left side and a block on the right side. The mechanisms were the same as explained above. Again, the tools stayed available throughout the entire session.

Black tape was wrapped around the tube (sides that needed to be operated by a stick) and platform (sides that needed to be operated by a block) to highlight the main features and make it easier for the apes to assess which tool needed to be used.

Apparatus ‘Stick-Stick’



Apparatus ‘Block-Block’



Apparatus 'Block-Stick'

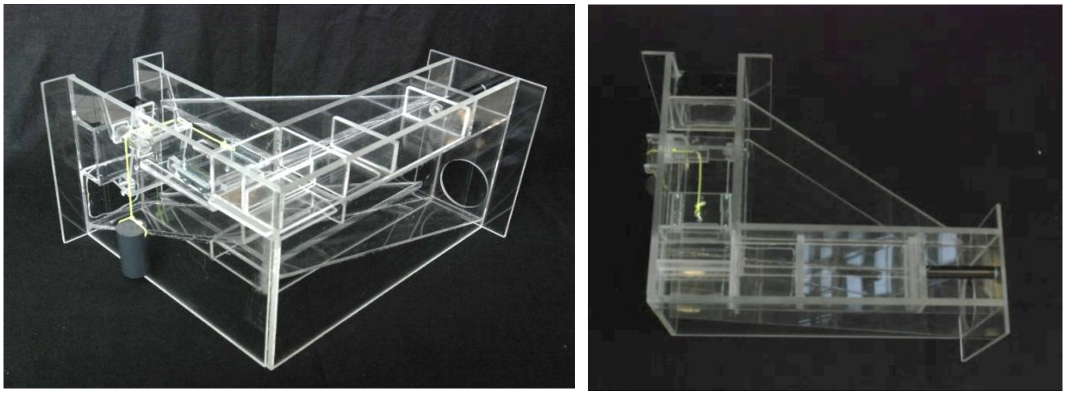


Figure 2.2 Picture of apparatuses that were used in the experiment 'Cooperation'. Each apparatus forms a 90° angle and thus could be attached to two cages simultaneously. The left side of the apparatuses was attached to the left cage and the right side to the right cage. Therefore, the apes who sat in adjacent cages could operate the respective apparatus at the same time. 'Apparatus Stick-Block' is not shown here because it was build in the same way as 'apparatus Block-Stick' except that the sides were switched. Black tape was used to make the specific feature (i.e. tube or opening) of the respective side more salient, here highlighted by the red circles.

3. Design

This study entails two different experiments consecutively presented to each dyad (see Figure 2.3). We started with experiment 'Helping' (hereafter, 'Helping 1'), in which tool transfers had no direct benefit for the helper. Subsequently, we presented each dyad with experiment 'Cooperation', in which transfers led to a direct benefit for the helper. To rule out order effects, we switched back to experiment 'Helping' (hereafter, 'Helping 2') for all dyads that transferred a tool at least once in experiment 'Cooperation', resulting in an ABA design for these dyads. Dyads that did not transfer a single tool in experiment 'Cooperation' received a knowledge control test.

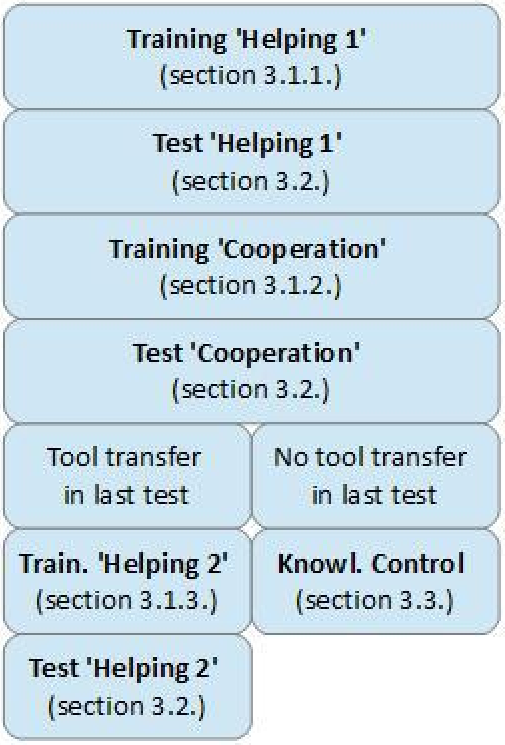


Figure 2.3 Flow-chart of the entire study design.

3.1. Training

Before each test, apes received an individual training to ensure that they understood the mechanisms and to ensure that helpers knew whether they could work independently of the receiver or not. During training, none of the apes was paired with a conspecific and never had to transfer a tool to a different cage in order to retrieve the rewards. The training merely consisted of familiarizing the individuals in how to use the tools on each apparatus.

3.1.1. Experiment 'Helping I'

Each ape individually received two consecutive training phases.

In the first phase, we familiarized the apes with the apparatuses and their respective tools. In order to provide initial support, we gave one exemplar of the correct tool type to the ape and baited the apparatus with one grape. The tool stayed available to the ape throughout the entire session and we only asked the ape to return it after the session was completed. We rebaited the apparatus with another grape once the ape successfully operated the apparatus and retrieved the previous grape. This procedure was repeated until the ape retrieved a maximum of 14 grapes or after five minutes had passed. If they did not retrieve 14 grapes within five minutes, these trials were given the next testing day while still adhering to the limit of 14 grapes and five minutes. In order to transfer to the next training phase, each ape had to successfully retrieve 35 grapes. Therefore, they received a minimum of three training days.

In the second phase of training, we familiarized the apes with the experimental set up of the test (see Figure 2.4A). In order to do so, we used two adjacent cages and presented the apparatus in one and the tools in the other cage. The sliding door between both cages stayed open throughout the entire session, thus, the individual was able to freely move back and forth. Instead of only offering one tool as we previously did, we offered the same set of tools they would receive during the test. Thus, if the 'apparatus Stick' was presented, the ape received two sticks and one block; and if the 'apparatus Block' was presented, the ape received two blocks and one stick (see Figure 2.4B). The given apparatus was baited with five grapes. First, we presented each individual with 'apparatus Stick' because the initial training was more distant for this apparatus. On the next day, we presented 'apparatus Block' and continued switching back and forth. One trial of the respective apparatus was given per day and each trial lasted three minutes independent of whether the given ape successfully retrieved the rewards or not. The ape passed into the test if she correctly manipulated the presented apparatus on three consecutive sessions. Correctly manipulating was defined as touching the apparatus with the correct tool only and successfully retrieving the rewards. We did not consider instances as failed when the incorrect tool was used after one minute had passed from the point that all grapes had been retrieved; rather this was considered as explorative or playful behaviour. The ape transferred into the test only when she passed the criterion for both apparatuses. In case she passed the criterion for one but not the other apparatus, we continued presenting the remaining apparatus on each testing day until she also passed the criterion for this apparatus.

Bonobos needed an average of 3.33 trials to reach criterion for 'apparatus Stick' (min: 3, max: 7) and 5 for 'apparatus Block' (min: 3, max: 7). Similarly, chimpanzees needed an average of 3.83 trials to reach criterion for ‘apparatus Stick’ (min: 3 max: 4) and 8 trials for ‘apparatus Block’ (min: 6, max: 10).

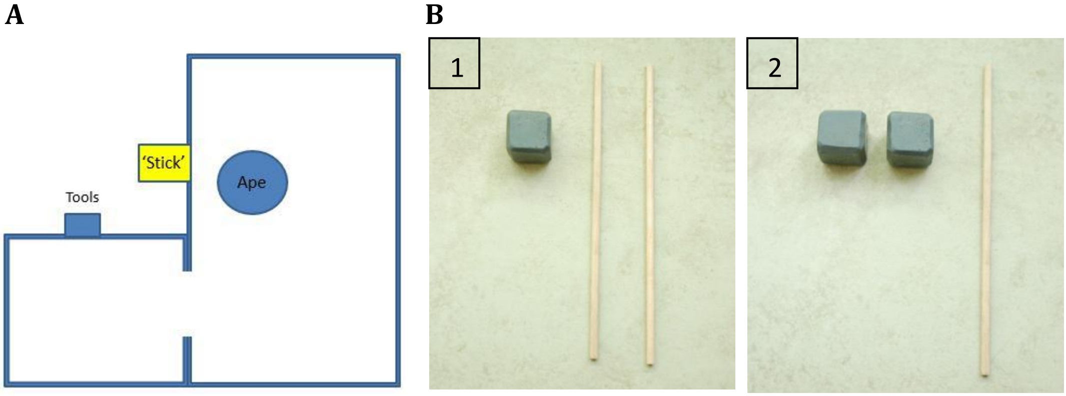


Figure 2.4 Set-up of the second training period, where the tools were presented in one cage and the apparatus (here ‘apparatus Stick’ but the same was true for ‘apparatus Block’) in an adjacent cage with the sliding door open (A). In case the ape received ‘apparatus Stick’, the assortment of tools shown in Figure B1 was given. Similarly, in case the ape received ‘apparatus Block’, the assortment of tools shown in Figure B2 was given. This way, there was always a spare tool of each type additional to the one the helper could use herself. Even though the tool was retrievable from the apparatus, we wanted to make sure that the apes did not perceive a negative cost in transferring that tool. Therefore, we offered an additional tool of the type they had to use themselves.

3.1.2. Experiment ‘Cooperation’

Each ape received only one individually presented training phase given that they already knew how to use the tools from experiment ‘Helping 1’.

The logic and procedure were the same as in the second training phase of experiment ‘Helping 1’ (refer to section 3.1.1.; p. 48). We familiarized the apes with the experimental set up of the test by attaching the given apparatus to both cages and presenting the assortment of tools in the left cage. The sliding door between both cages stayed open throughout the entire session, thus, the individual was able to freely move back and forth. If ‘apparatus Stick-Stick’ or ‘apparatus Stick-Block’ was presented the ape received two sticks and one block, if ‘apparatus Block-Block’ or ‘apparatus Block-Stick’ was presented the ape received two blocks and one stick (see Figure 2.4B). The apparatuses were baited with ten grapes, five of which could roll towards the left and five towards the right cage.

First, we presented each individual with ‘apparatus Block-Block’, ‘apparatus Stick-Block’, and ‘apparatus Block-Stick’. On the next day, we presented ‘apparatus

Stick-Stick', 'apparatus Block-Stick', and 'apparatus Stick-Block'. We then continued switching back and forth while changing the order within each day in a counterbalanced fashion. One trial of the respective apparatus was given per day and each trial lasted three minutes independent of whether the given ape successfully retrieved the rewards or not. The ape passed into the test if she correctly manipulated both sides of the presented apparatus on three consecutive sessions. Correctly manipulating was defined as touching the given side of the apparatus with the correct tool only and successfully retrieving the rewards. We did not consider instances as failed when the incorrect tool was used after one minute had passed from the point that all grapes had been retrieved; rather this was considered as explorative or playful behaviour. The ape transferred into the test only when she passed the criterion for all four apparatuses. In case she passed the criterion for some but not all apparatuses, we continued presenting the remaining apparatus or apparatuses until she passed the criterion for all.

Bonobos needed an average of 4.17 trials to reach criterion for 'apparatus Stick-Stick' (min: 3, max: 5), 9.17 for 'apparatus Stick-Block' (min: 3, max: 15), 10.83 for 'apparatus Block-Stick' (min: 6, max: 14), and 8.5 for 'apparatus Block-Block' (min: 7, max: 11). Similarly, chimpanzees needed an average of 3.17 trials to reach criterion for 'apparatus Stick-Stick' (min: 3 max: 4), 9.67 trials for 'apparatus Stick-Block' (min: 6, max: 12), 11 trials for 'apparatus Block-Stick' (min: 6, max: 16), and 10.17 trials for 'apparatus Block-Block' (min: 7, max: 16).

3.1.3. Experiment 'Helping II'

To make sure that the helpers knew that they again could work independently of the receiver, they first had to complete three trials of the second training phase of experiment 'Helping 1' before transferring to the test for each apparatus (refer to section 3.1.1.; p. 48). All subjects correctly operated each apparatus, except for one female who incorrectly operated 'apparatus Block' on the second trial. Additionally, one female used the stick instead of her hands to rake in the grapes after she successfully operated 'apparatus Block'. We still assumed that they were able to flexibly operate each apparatus.

3.2. Test

Each ape was tested with two different partners, and was assigned the role of the helper with one and the role of the receiver with the other partner. Both conspecifics of a dyad sat in adjacent cages with the sliding door closed. A mesh separating the two cages allowed for any interactive behaviours and visibility into the cage of the conspecific. In experiment ‘Helping’, both apparatuses were baited with five grapes each. In experiment ‘Cooperation’, the apparatus was baited with ten grapes, five of which could roll towards the helper and five towards the receiver. Even though both conspecifics needed a tool, only the ape labelled as helper received access to an assortment of tools. Thus, the helper needed to share a tool with the receiver in order for the receiver to operate her apparatus (experiment ‘Helping’) or her side of the connected apparatus (experiment ‘Cooperation’). In experiment ‘Helping’, the apparatuses were not connected and could be operated separately, therefore the helper could retrieve the own rewards independent of whether the receiver was able to access her rewards. Given that in experiment ‘Cooperation’ both sides had to be operated to release the rewards, the helper now needed to share a tool with the receiver in order for both individuals to receive any rewards. This induced an incentive for the helper to share a tool with the receiver and was the main difference to experiment ‘Helping’. The helper was always given access to an assortment of three tools (see Figure 2.4B). The assortment corresponded to the type of apparatus presented to the helper, which meant we gave two tools of the type that she could use on her side and one tool of the other type. Even though the tool she needed herself was retrievable from the apparatus after using it, we wanted to make sure that the apes did not perceive a negative cost in transferring that tool as they might have attributed more value to a tool they used than to one they did not need. Therefore, we offered an additional tool, so there was always a spare tool of each type.

We used three conditions in both experiments. In the *condition ‘Same’*, both conspecifics were presented with the same type of apparatus, hence in experiment ‘Helping’ both received either a duplicate of ‘apparatus Stick’ or ‘apparatus Block’ (see Figure 2.5) and in experiment ‘Cooperation’ they received ‘apparatus Stick-Stick’ or ‘apparatus Block-Block’ (see Figure 2.6). Given that the assortment of tools was dependent on the type of apparatus presented to the helper (e.g. if the helper received 'apparatus Stick' or 'apparatus Stick-Stick' she was given two sticks and one block), the chance of randomly transferring the tool needed by the receiver was 2/3, since both need the same tool. In the *condition 'Different'*, both conspecifics were presented with the opposite type of apparatus (see Figure 2.5 and 2.6). Thus, in experiment 'Helping' one conspecific was presented with 'apparatus Stick' and the other conspecific with 'apparatus Block', or vice versa, and in experiment 'Cooperation', they were presented with 'apparatus Block-Stick' and 'apparatus Stick-Block'. The chance of randomly transferring the tool needed by the receiver was 1/3 in this condition, since only one out of the three tools presented was useful to the receiver (e.g. if the helper received 'apparatus Stick' or 'apparatus Stick-Block' she was given two sticks and one block from which the receiver could only use the block). In the *control condition*, we presented each of the four different scenarios that we used in the test conditions (see Figure 2.5 and 2.6). The only difference to the two test conditions was that the receiver was now also given access to a separate assortment of tools, where the combination of tools was dependent on the type of apparatus presented to the receiver. Therefore, there was no need for the helper to share a tool with the receiver as she could access her apparatus or side of the apparatus with the tools given to her. Dyads received twelve trials in each condition, and one trial of each of the three conditions was given per testing day. Thus, on day one they received one trial of condition 'Same', one trial of condition 'Different', and one trial of the control condition. The order was randomized and the same testing schedule that was given to the bonobo dyads was later also given to the chimpanzee dyads. Each trial lasted three minutes independent of whether the respective helper transferred a tool or not.

Condition 'Same'

Condition 'Different'

Control

Figure 2.5 Set up of the three conditions included in experiment 'Helping'. The helper was sitting in the left and the receiver in the right room. Both conspecifics received the same type of apparatus in the condition 'Same' and different types of apparatuses in the condition 'Different'. In both these test conditions, only the helper was given access to an assortment of tools. In the control condition, both conspecifics were given access to an assortment of tools. A grey box covered the tools and blocked the conspecific's view to inhibit targeted requesting gestures, but they were visible and easily accessible by the given individual in that room.

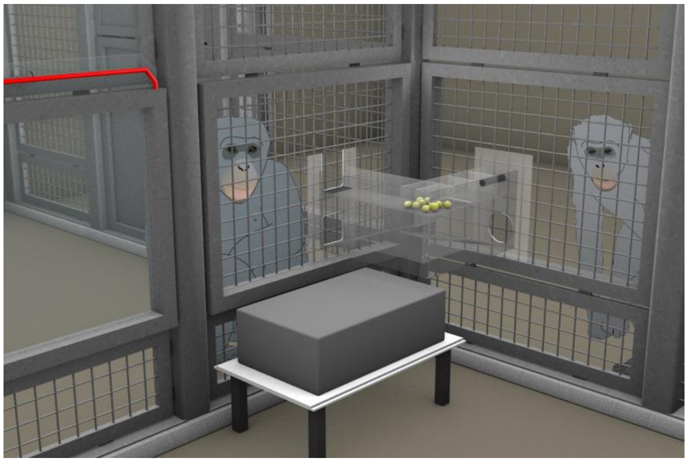


Figure 2.6 Set up of experiment 'Cooperation'. Condition 'Different' is visualized here but the same set up was used for condition 'Same' and the control condition (see Figure 2.5).

3.3. Knowledge Control

All helpers that did not share a tool in experiment ‘Cooperation’ received twelve trials, in which they had to operate the four different apparatuses of experiment ‘Cooperation’ by themselves (i.e. three trials per apparatus) instead of continuing with experiment ‘Helping 2’. We implemented this knowledge control to understand if tool transfers were not done in experiment ‘Cooperation’ because helpers failed to understand that both sides had to be operated or because they were not able to perceive the task as collaborative. The knowledge control adhered to the same procedure as the training of experiment ‘Cooperation’ (see section 3.1.2.; p. 49).

One of the two bonobo helpers that did not share tools was correct on all three trials for each of the four apparatuses (see Table 2.2). The other bonobo helper incorrectly operated ‘apparatus Block-Block’ on one trial and ‘apparatus Stick-Block’ on two out of three trials.

Chimpanzee helpers were correct on all three trials when operating ‘apparatus Stick-Stick’ (see Table 2.2). One individual incorrectly operated ‘apparatus Block-Block’ in one out of three trials, one individual incorrectly operated ‘apparatus Stick-Block’ in two out of three trials, and two individuals incorrectly operated ‘apparatus Block-Stick’ in one and all three trials, respectively.

As was discussed, some individuals made mistakes during this test. However, the overall frequency was low and we did not detect individual differences or general problems with specific apparatuses. We are therefore confident that helpers understood the general mechanism. Thus, even though these helpers did not share a tool they seemed to efficiently and flexibly operate the apparatuses by themselves.

Table 2.2 Overview of the success for each apparatus and subject during the knowledge control.

Subject	'apparatus Stick-Stick'	'apparatus Block-Block'	'apparatus Stick-Block'	'apparatus Block-Stick'
Kuno, Bonobo	3/3	2/3	1/3	3/3
Luiza, Bonobo	3/3	3/3	3/3	3/3
Kara, Chimp	3/3	3/3	3/3	3/3
Fraukje, Chimp	3/3	3/3	3/3	0/3
Lome, Chimp	3/3	3/3	1/3	3/3
Lobo, Chimp	3/3	3/3*	3/3	3/3*
Kofi, Chimp	3/3	3/3	3/3	3/3
Sandra, Chimp	3/3	2/3	3/3	2/3

*used the stick instead of finger to push forward the block on one trial

4. Data coding

We coded whether tool transfers occurred, the order in which each tool type was transferred during a given session, and four distinct behaviours that could have been potentially exhibited by the receiver (i.e. scratching, banging, reaching, and staying in close proximity). We scored for each second of a given trial whether any of the behaviours occurred. Transfers were considered when a tool initially given to the helper was directly transferred to the cage of the receiver by the helper, or when the receiver was allowed to grab a tool close to the mesh (such tolerated theft occurred in two cases). To assess the level of negative arousal, we coded the occurrence of scratching and banging (Rosati & Hare, 2013). Scratching was operationalized as "rake one's own hair or skin with fingernails including large movements of arm" (Baker & Aureli, 1997, p. 1036). Banging was operationalized as using either hands or feet to hit the mesh separating the recipient from the helper or the mesh onto which the apparatus is mounted. To understand whether receivers made an effort to acquire tools from the helper, we coded the occurrence of reaching. Reaching was operationalized as putting at least one finger through the mesh, which separated the cages of two conspecifics. Finally, we included maintaining close proximity as a measure of whether the receiver tried to stay close to the helper. In case requesting gestures were exhibited only rarely, this measure enabled us to understand if the receiver did not gesture even though she was attentive to the helper's actions or if she did not pay attention to the helper at all. We operationalized close proximity as the time spent in a maximum distance of 50cm to the mesh separating the two conspecifics.

To assess interrater reliability, we randomly selected 20% of the bonobo data (59 sessions) that was coded by a research assistant blind to the procedure and hypotheses. We selected the bonobo data only given that nearly all models are based on this data. To assess the four behavioural variables (reaching, close proximity, scratching, and banging) we used Cohen's Kappa to compare whether for each second (0-180) of a session the two raters agreed that any of the variables occurred. We acquired sufficient and good reliability for each of the four behavioural variables (Reaching: K = 0.72; Close proximity: K = 0.93; Scratching: K = 0.80; Banging: K = 0.73). Additionally, we assessed whether the two raters agreed on the type of tool that (if any) was shared during a session. Again we acquired sufficient reliability (K = 0.89).

5. Analyses

We analysed the data from three different perspectives: 1) what factors influenced the likelihood that helpers transferred tools, 2) whether the behaviour of the receivers differed between species and upon receiving the correct tool, and 3) whether helpers were able to tailor their prosocial acts according to the needs of the receiver.

5.1. Tool transfers

Since across all sessions and dyads, chimpanzees only transferred a tool twice, we based the main analyses only on the data of the bonobos to assess the factors influencing tool transfers. We fitted a Generalized Linear Mixed Model (GLMM; Baayen, 2008) with a binomial error structure and logit link function (McCullagh & Nelder, 1989) and used the occurrence of at least one transfer (Yes, No) in a given session as our response variable. The number of observations was 576 of six dyads.

To understand whether it made a difference if helpers benefitted from transferring a tool and whether there were order effects present, we used the type of experiment with three levels (‘Helping 1’, ‘Cooperation’, ‘Helping 2’) as one of our predictors. Additionally, we included condition as a predictor with three levels (‘Same’, ‘Different’, ‘Control’) to understand whether helpers transferred tools irrespective of whether the receiver actually needed a tool. In such a case we would observe a similar frequency of transfers in the control condition as in the two test conditions. The z-transformed (Ragazzini & Zadeh, 1952) predictor session number was included in order to assess whether helpers were more likely to transfer tools at the beginning, middle, or end of the experiment indicating either motivational issues or time needed to understand the task. To understand how this factor was interacting with the predictor experiment we also included an interaction term of these two factors. This interaction term informs about whether the effect of session number on the response was different for one of the given experiments. Hence, whether motivational factors were influencing the helpers to different degrees depending on whether they benefitted versus not benefitted from helping. Finally, we included the predictor reaching with two levels (Yes, No) to understand how reaching by the receiver influenced the probability of a transfer. These four predictors and the interaction term described above were used as key predictors and added to the model as fixed effects.

As a further fixed effect we included the interaction term between the age of the helper and the age of the receiver and the two respective main effects. Both variables were z-transformed (Ragazzini & Zadeh, 1952) before we included them in the model. The interaction term was added to control for any influences that the age of the receiver and helper together might have had on the likelihood of transfers (i.e. older individuals might have shared more tools when the receiver was young).

To keep type 1 error rates at the nominal level of 5%, we also included the random intercepts (Barr, Levy, Scheepers, & Tily, 2013; Forstmeier & Schielzeth, 2011) for test day and dyad identity, and the random slopes components (Barr et al., 2013; Forstmeier & Schielzeth, 2011) within dyad identity for the fixed effects experiment, condition, reaching, session number, the interaction between experiment and session number, age of the helper, age of the receiver, and the interaction between age of the helper and age of the receiver. In order to do so, the fixed effects experiment, condition, and reaching were manually dummy coded and then centered, and the fixed effects session number, age of the helper, and age of the receiver were z-transformed (Ragazzini & Zadeh, 1952).

5.2. Receivers' behaviours

We further investigated whether the two species differed in terms of the behaviour executed by the receivers and if this might have explained the difference in transfers done by the helpers. We initially fitted linear mixed models (LMM; Baayen, 2008) with a Gaussian error structure and identity link function, separately for each behaviour (i.e. scratching, banging, requesting, and close proximity) expressed by the receivers. However, none of the models met the required assumptions of homoscedasticity of the models' residuals. This was due to the fact that we had too many zeros in the data. Thus, we fitted GLMMs (Baayen, 2008) with a binomial error structure and log link function. Again, this was done separately for each behaviour (i.e. scratching, banging, requesting, and close proximity) expressed by the receivers. Our response variable was whether the respective variable occurred in a given session (Yes, No) and our only predictor was the variable species (Bonobo, Chimpanzee). Given that close to no tools were shared by chimpanzees but bonobos already shared substantially more tools in experiment 'Helping 1', frustration might have already influenced chimpanzee receivers differently than bonobo receivers in experiment 'Cooperation'. Therefore, we only focused on the data from the experiment 'Helping 1' as this seemed to be most comparable. For each GLMM, the number of observations was 430 of twelve dyads.

As a further fixed effect we included the z-transformed (Ragazzini & Zadeh, 1952) predictor session number to control for any effects that mere time passing might have had on the expression of the respective behaviour. Additionally, we included the factor condition with three levels ('Same', 'Different', 'Control') to control for the fact that the two test conditions most likely induced a different response than the control condition. Finally, we included the interaction term between the age of the helper and the age of the receiver and the two respective main effects to control for any influences that the age of the receiver and helper together might have had on the expression of any of the behaviours (e.g. younger individuals might have reached more when the helper was old). Both variables were z-transformed (Ragazzini & Zadeh, 1952) before being included in the model.

To keep type 1 error rates at the nominal level of 5%, we also included the random intercepts for test day and dyad identity. We included the random slopes components (Barr et al., 2013; Forstmeier & Schielzeth, 2011) within dyad identity for the fixed effects condition and session number, and the random slopes components (Barr et al., 2013; Forstmeier & Schielzeth, 2011) within test day for the fixed effects species, the interaction between the helpers' and receivers' age, and their main effects. In order to do so, each of the factors was manually dummy coded and then centered, and the each of the covariates was z-transformed (Ragazzini & Zadeh, 1952).

Furthermore, we investigated whether any of the behaviours executed by the receiver were more likely to occur before versus after the correct tool was shared. This deepens our understanding of why the receivers behaved in the observed manner and rules out the possibility that, for example, reaching and transfers were merely coinciding in a given session but were not preceding each other. We again only used the data of the bonobos given that the chimpanzees only transferred two tools, and fitted a GLMM (Baayen, 2008) with a binomial error structure and logit link function (McCullagh & Nelder, 1989). Our response variable was whether the behaviour occurred in a given session (Yes, No), in which a correct tool was transferred, indicated separately for the periods before and after the correct tool transfer and separately for each behaviour that we considered in this model (i.e. reaching, scratching, and staying in close proximity). We did not include the behaviour banging as it was only executed by one individual. Furthermore, only sessions in which a correct tool was eventually shared were included in this analysis and incorrect tools that were shared first were ignored. The rationale behind this is that the need of receiving a tool was only fulfilled if a correct tool was shared. In case no or an incorrect tool was shared it would have been sensible for the receiver to continue begging. The number of observations was 696 of four dyads. Our key predictor was the variable 'before versus after the correct tool transfer' (hereafter, 'before versus after') to understand whether acquiring the correct tool indeed influenced the occurrence of receivers' behaviours. Additionally, we included the type of behaviour with three levels (reaching, scratching, close proximity) and its interaction 'before versus after' into the model. This interaction term informs about whether for any of the behaviours the effect of 'before versus after' is different than for any of the other behaviours. To give an example, even though scratching might occur significantly less often after than before a correct tool is shared, reaching might in comparison occur even significantly less often after than before that transfer. If the interaction term is not significant but only the main factor assessing the effect 'before versus after', it means the probability of each behaviour being executed by the receiver is significantly different before and after the transfer but to the same degree. We included an offset term (McCullagh & Nelder, 1989) to account for the fact that the duration of the periods before and after the transfer differed from one another and also between trials, as the tool was not shared to the exact same time across sessions. The durations were log-transformed in order to add the offset term. These two predictors and their interaction described above are used as key predictors and added to the model as fixed effects.

As an additional fixed effect, we used condition with two levels ('Same', 'Different') to control for any effects that the difference in test conditions might have had on the receiver. We did not use the condition 'Control' because any of the behaviours should not have been executed for the reason of acquiring tools given that the receiver also had access to tools. Additionally, we included experiment with three levels ('Helping 1', 'Cooperation', 'Helping 2') to control for the fact that probabilities of the behaviours' occurrence differed between the three experiments given that there was an incentive to share tools in experiment 'Cooperation'. Moreover, we included the z-transformed (Ragazzini & Zadeh, 1952) variable session number to control for the possibility that over time the probability of the receivers showing certain behaviours might have in- or decreased. Finally, we included the interaction between the age of the helper and the age of the receiver and the two respective main effects. Both variables were z-transformed (Ragazzini & Zadeh, 1952) before they were included in the model. As in the previous models, this interaction was added to control for any influences that the age of the receiver and helper together might have had on the likelihood that the receiver executed any of the behaviours.

To keep type 1 error rates at the nominal level of 5%, we included the random intercepts (Barr et al., 2013; Forstmeier & Schielzeth, 2011) for dyad identity, test day identity, and trial identity. Moreover, we included the random slopes components (Barr et al., 2013; Forstmeier & Schielzeth, 2011) within dyad identity for the factors behaviour, 'before versus after', experiment, condition, session number, age of helper, age of receiver, the interaction between behaviour and 'before versus after', and the interaction between age of helper and age of receiver. Second, we included the random slopes components within test day identity for the predictors behaviour, 'before versus after', condition, and the interaction between behaviour and 'before versus after'. Third, we included the random slopes components within trial identity for the predictors behaviour, 'before versus after', and the interaction between behaviour and 'before versus after'. In order to do so, the fixed effects behaviour, 'before versus after', experiment, and condition were manually dummy coded and then centered, and the fixed effects session number, age of the helper, and age of receiver were z-transformed (Ragazzini & Zadeh, 1952).

To then further understand whether the possible effect of the variable 'before versus after' was merely apparent because any tool was shared, we fitted the exact same model but looked at whether the behaviours occurred before versus after an incorrect tool was shared in a given session. Thus, the same key and control predictors and random intercept and slope components were used, while the response variable now considered instances of an incorrect transfer instead of correct transfer in that session.

5.3. How did the helper select the tools?

Finally, we assessed how bonobo helpers selected the first tool that they transferred in order to understand whether the tools were selected according to the others' needs. We fitted a GLMM (Baayen, 2008) with a binomial error structure and logit link function (McCullagh & Nelder, 1989) and our response variable was whether the first transfer in a given session, in which a transfer occurred, was correct and had two levels (Yes, No). Therefore, only the first transfer in a given session was considered and all second or third transfers were discarded. The number of observations was 135 of four dyads. To assess whether the type of experiment influenced the occurrence of correct first transfers, we included the predictor experiment with three levels ('Helping 1', 'Cooperation', 'Helping 2'). This was done to understand whether helpers might have paid more attention to the needs of the receiver when they themselves benefitted from transferring the correct tool (i.e., in experiment 'Cooperation'). We included the predictor condition with two levels ('Same', 'Different') to understand whether one of the two conditions might have been easier for the helper, for example, if they both needed the same tool. We used a log-transformed offset term (McCullagh & Nelder, 1989) to account for the fact that the chance of transferring the correct tool was different between the two conditions since the helper always received two tools of the type she needed herself and one of the remaining type. Thus, in the condition 'Same', in which both needed the same tool, the chance of transferring the correct tool was 2/3. In comparison, the chance of transferring the correct tool in the condition 'Different' was 1/3 since the receiver needed a different tool than the helper. Finally, we included a predictor specifying which tool the receiver needed in a given session with two levels ('Stick', 'Block') to understand whether the helper was preferably transferring a specific type of tool. These three predictors described above were used as key predictors and added to the model as fixed effects.

As a further fixed effect, we included the z-transformed (Ragazzini & Zadeh, 1952) variable age of the helper to control for any influences that it might have had on the probability to transfer the correct tool. Additionally, we included the z-transformed (Ragazzini & Zadeh, 1952) variable session number to control for any learning effects that might have influenced the ability to transfer the correct tool.

To keep type 1 error rates at the nominal level of 5%, we also included the random intercepts (Barr et al., 2013; Forstmeier & Schielzeth, 2011) for test day and dyad identity, and the random slopes components (Barr et al., 2013; Forstmeier & Schielzeth, 2011) within dyad identity for the fixed effects experiment, condition, tool of the receiver, session number, and age of the helper. In order to do so, the fixed effects experiment, condition, and tool of the receiver were manually dummy coded and then centered, and the fixed effects session number and age of the helper were z-transformed (Ragazzini & Zadeh, 1952).

Given that all the key predictors of the model had a nonsignificant influence on the response, we continued to manually dummy code and then center each categorical predictor. We then calculated two new GLMMs while maintaining the same structure as in the initial model, except that in one model we used the condition ‘Same’ as a reference and in the other the condition ‘Different’. Further, we used an intercept optimization (the R-function was written by Roger Mundry and is available upon request) on these two new models. The resulting intercept was assessed to gauge the average probability of correct first transfers while controlling for the effect of each predictor in the model. Finally, the respective intercepts were tested against a chance level of 2/3 (condition ‘Same’) and 1/3 (condition ‘Different’) to understand if transfers were done randomly in one or both test conditions while controlling the influences of the other factors in the model.

5.4. General information for each model

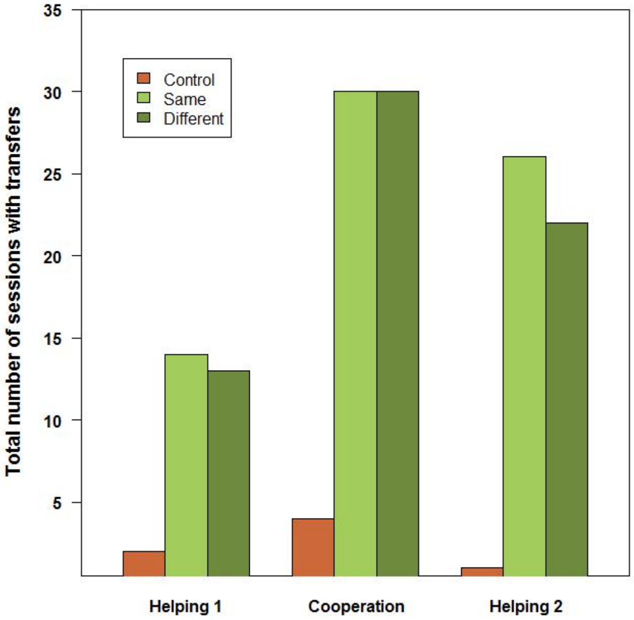
Each of the models discussed above was fitted in R (version 3.4.0; R Core Team, 2017) using the function glmer (and lmer for the linear mixed models) provided by the package ‘lme4’ (Bates, Maechler, Bolker, & Walker, 2015) and with the level of significance set to 0.05. To check the overall significance of the respective key predictors, we ran a likelihood ratio test that compared the full model with a null model from which the key predictors were omitted (Forstmeier & Schielzeth, 2011). Only if the comparison between the full and null model reached significance did we investigate the effect of the individual key predictors. To rule out collinearity, we inspected Generalized Variance Inflation Factors (GVIF; Fox & Weisberg, 2011) of a respective model from which we excluded the random effects and possible interactions. The function vif provided by the R package ‘car’ was used (Fox & Weisberg, 2011) and revealed no collinearity problem with any of our models (maximum VIF = 1.16; Zuur, Ieno, & Elphick, 2010). Finally, we investigated whether the model parameters obtained from the full model were stable by excluding the random effects one at a time from the data (the R-function was written by Roger Mundry and is available upon request). Comparing the model parameters with those obtained by excluding levels of the random effects one at a time showed that the model parameters were fairly stable and no influential cases existed in each of the models. However, there was one exception to this: The GLMM investigating whether there was a species difference in likelihood that individuals banged against the mesh was unstable (orig. = 23.6, min. = -10.53, max. = 46.80) and has to be interpreted with caution. This instability is due to a generally low number of sessions in which bonobos banged against the mesh.

C. Results

1. Tool transfers

Bonobo helpers shared a tool in 142 sessions across all conditions and experiments, and more often in both test conditions than the control (see Figure 2.7A). Most tools were shared in experiment 'Cooperation', in which helpers were given an incentive. Helpers frequently transferred more than one tool in a given session. The total number of tool transfers was 246, with 122 occurring in the condition 'Same', 115 in the condition 'Different', and 9 in the control condition across all three experiments. Four of the six bonobo dyads contributed to the number of observed transfers and in each dyad we found a similar pattern of mainly sharing in the two test conditions (see Figure 2.7B). These four pairs were composed solely of females, one being a mother-infant dyad. No transfers were observed in the mixed-sex bonobo pairs.

A



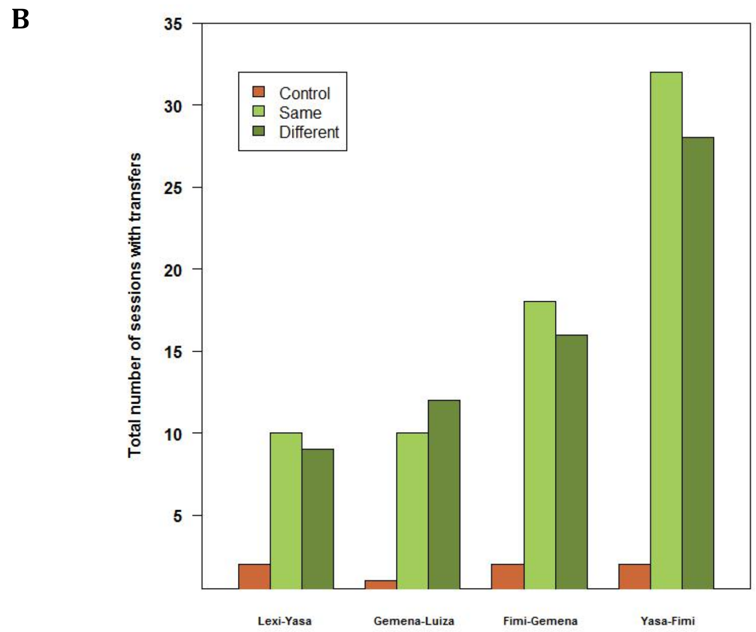


Figure 2.7 Number of sessions with at least one tool transfer in each of the three conditions for each experiment (A) and for each dyad across all experiments (B). Across all three experiments, each dyad received a total of 36 sessions in each condition. Pair "Yasa-Fimi" is the mother-infant dyad.

The transfer frequency of bonobo helpers stands in contrast to a total of two instances, in which one out of six chimpanzee helpers shared a tool. This dyad was a mother with her sub-adult daughter and both transfers occurred in the condition 'Same' in experiment 'Helping 1'. Since none of the chimpanzee helpers shared a tool in experiment 'Cooperation', we did not switch back to experiment 'Helping 2'.

To assess the factors influencing tool transfers, we based the main analyses only on the data of the bonobos since across all sessions and dyads chimpanzees only transferred a tool twice. Comparing the GLMM that included the key predictors condition, reaching, and the interaction between session and experiment with a model only comprised of the control factors and random intercepts and slopes showed that the predictors together significantly contributed to explaining whether a transfer occurred, $p < .001$ ($\chi^2 = 66.76$, $df = 8$, $N = 576$; see Table 2.3). Bonobo helpers shared a tool significantly more often in the two test than the control condition and, hence, were sensitive to whether the receiver was actually in need of a tool ($\chi^2 = 26.93$, $df = 2$, $p < .001$). We also found a significant interaction between the type of experiment presented to the dyads and the corresponding session number ($\chi^2 = 13.7$, $df = 2$, $p = .001$). The interaction indicates that the effect of session number on the probability of a transfer occurring differed depending on the type of experiment. Transfers were done randomly across all sessions when helpers did not benefit from sharing a tool (Figure 2.8A & 2.8C). However, when helpers did benefit the probability of a transfer increased over the course of the experiment (Figure 2.8B). Reaching by the receiver significantly influenced the probability that a helper transferred a tool in a given session ($\chi^2 = 5.77$, $df = 1$, $p = .016$).

Table 2.3 Results of GLMM assessing what variables influenced the occurrence of tool transfers in bonobo dyads.

Term	Estimate	SE	lower CI	upper CI	*Z*	*P*
Intercept	-6.88	1.53	-11.21	4.17	(3)	(3)
Experiment						
Helping 1 vs Cooperation	-2.85	0.62	-4.27	-1.36	(3)	(3)
Helping 2 vs Cooperation	-0.55	0.48	-1.54	0.43	(3)	(3)
Session(1)	2.27	0.41	1.54	3.21		
Condition					26.93(2)	<.001(2)
Same vs Control	4.65	0.76	3.29	6.34	(3)	(3)
Different vs Control	4.42	0.73	3.13	6.04	(3)	(3)
Reaching						
Yes vs No	1.02	0.42	0.22	1.90	5.77(2)	.016(2)
Experiment*Session(1)					13.7(2)	.001(2)
Helping 1 vs Cooperation	-1.59	0.53	-2.75	-0.59	(3)	(3)
Helping 2 vs Cooperation	-2.08	0.50	-3.19	-1.15	(3)	(3)
Age Helper(1)	-3.75	1.64	-7.82	2.22	(3)	(3)
Age Receiver(1)	-1.49	2.09	-9.08	3.61	(3)	(3)
Interaction(1)						
Age Helper*Age Receiver	-1.33	1.45	-5.32	1.55	0.92(2)	.338(2)

(1) standardized to its mean
(2) overall effect of the predictor
(3) not shown because of limited interpretation

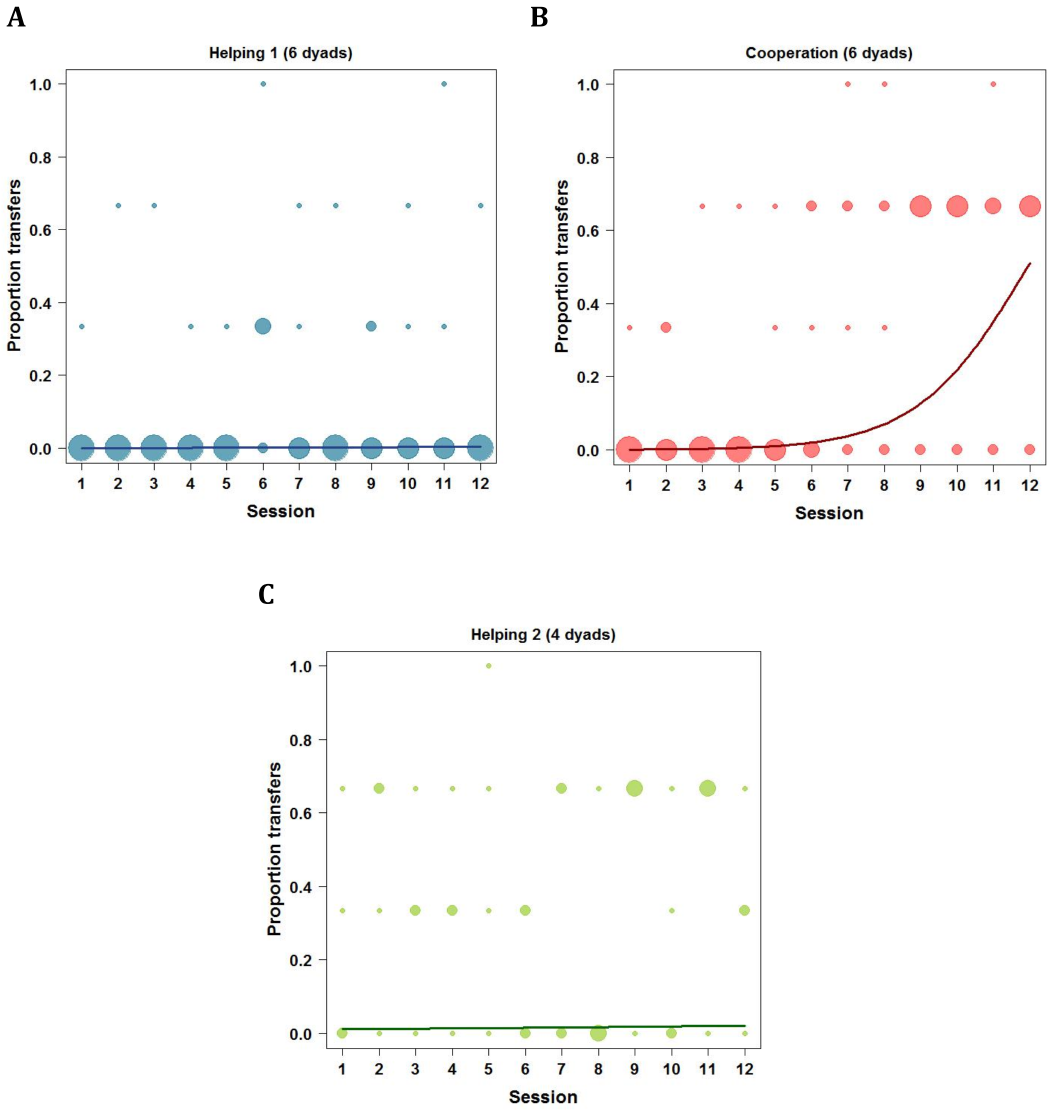


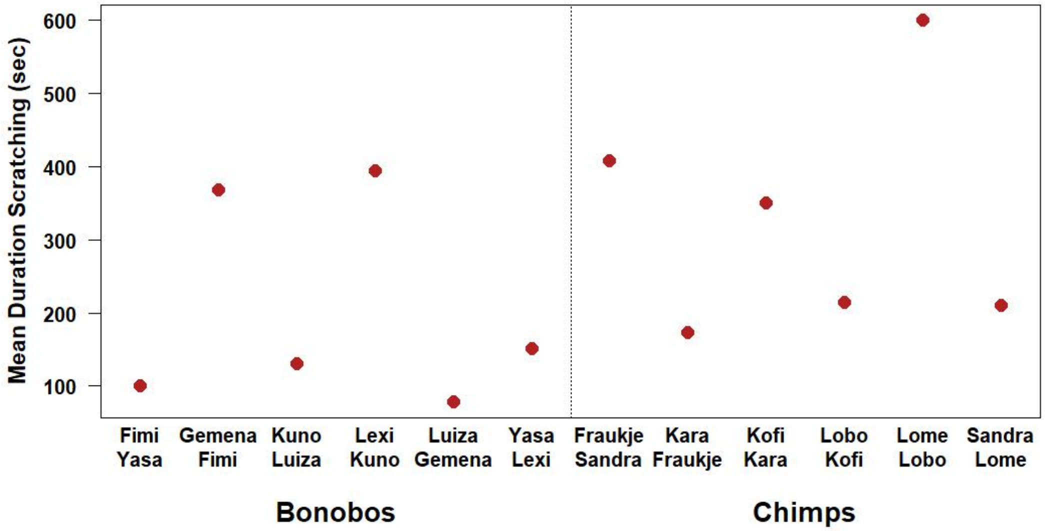
Figure 2.8 Proportion of transfers across the three conditions within each session separately plotted for experiment 'Helping 1' (A), 'Cooperation' (B), and 'Helping 2' (C). Proportions being 0 denote helpers that did not share a tool in any of the three conditions. Proportions being 0.33 denote helpers that only shared in one condition on that session. Similarly, proportions being 0.66 denote helpers that shared a tool in two conditions on that session. Finally, proportions being 1 denote helpers that shared a tool on all three conditions on that session. The larger the area of the points, the more helpers acted in such a manner on the same session. To give an example, we know that helpers shared a tool twice in the control condition in experiment 'Helping 1' (see Figure 2.7A) and can infer from this figure that the helper also shared a tool in both test conditions during session six and eleven, as proportions being 1 denote helpers that shared a tool on all three conditions on a given session. Similarly, we know that helpers shared a tool on six sessions in the control condition in experiment 'Cooperation' (see Figure 2.7A) and can infer from this figure that on three of such occasions they also shared a tool in both test conditions while they did not on the other three occasions. The interaction of session and experiment can be visually assessed as transfers were done randomly across sessions in experiment 'Helping 1' and 'Helping 2' but increased to a consistent level around session 6 in experiment 'Cooperation'. From previous assessments (see Figure 2.7A) we know that these transfers mainly occurred in the two test conditions.

2. Receivers' behaviours

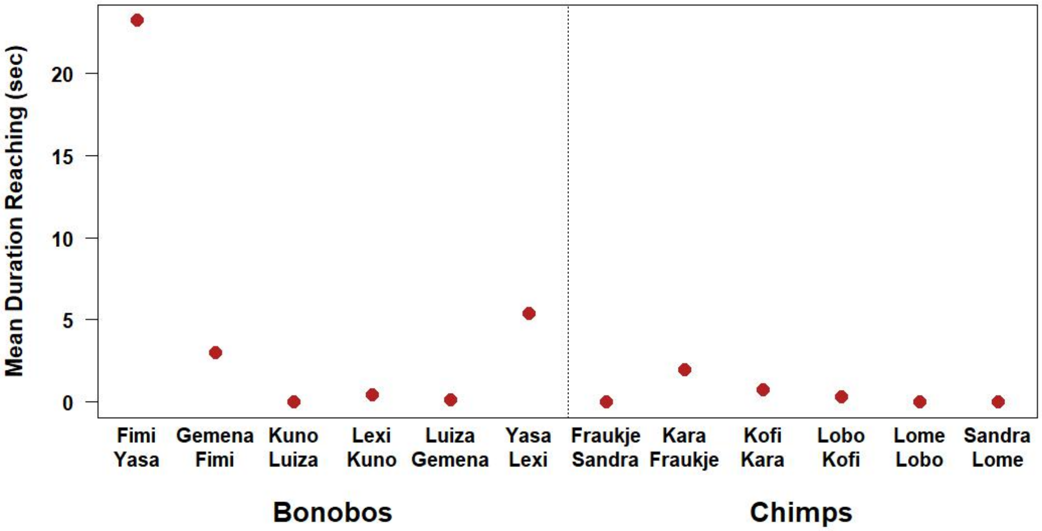
We further wanted to understand 1) whether receivers of the two species behaved differently to one another and 2) whether bonobo receivers changed their behaviour upon acquiring the correct tool.

Figure 2.9 depicts the total mean duration that each pair exhibited the four behaviours. Bonobos and chimpanzees only significantly differed with regard to whether receivers scratched themselves at least once during a session ($\chi^2 = 7.47$, $df = 1$, $N = 432$, $p = .006$; see Table 2.4), but did not significantly differ to bonobos in any of the other behaviours that we coded. The GLMM that assessed whether receivers of the two species reached more often at least once during a session was not significant ($\chi^2 = 2.67$, $df = 1$, $N = 432$, $p = .102$; see Table 2.5). We also did not find a difference regarding close proximity ($\chi^2 = 0.01$, $df = 1$, $N = 432$, $p = .905$; see Table 2.6) and banging ($\chi^2 = 1.77$, $df = 1$, $N = 432$, $p = .184$; see Table 2.7). The standard errors of the model that investigated the effect of banging were very large due to the general infrequency of banging by bonobo receivers. Thus, the model result is somewhat uncertain. In general, however, behavioural differences seem not sufficient to explain the lack of transfers from chimpanzee helpers.

A

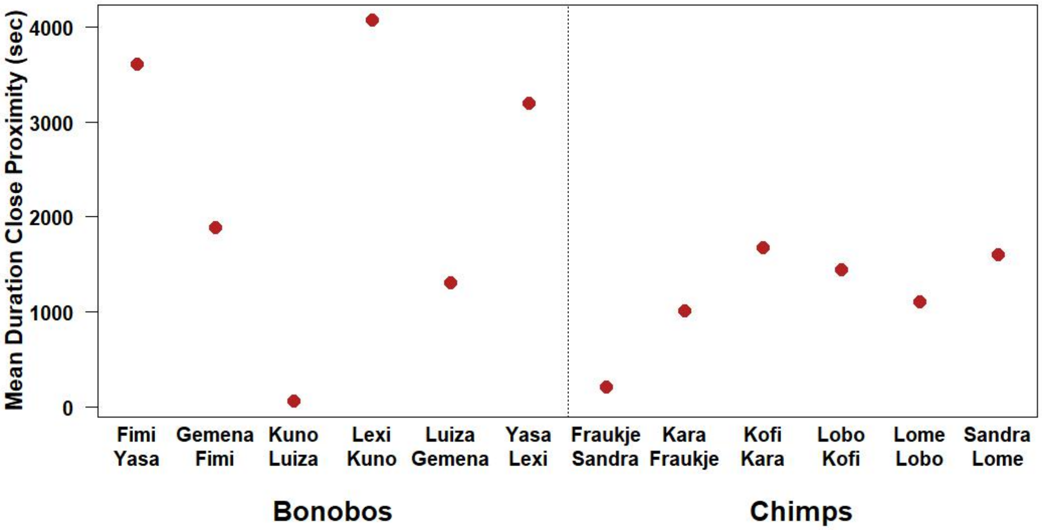


B



Mean Duration Reaching (sec)
0
5
10
15
20
Fimi Yasa
Gemena Fimi
Kuno Luiza
Lexi Kuno
Luiza Gemena
Yasa Lexi
Fraukje Sandra
Kara Fraukje
Kofi Kara
Lobo Kofi
Lome Lobo
Sandra Lome
Bonobos
Chimps

C



Mean Duration Close Proximity (sec)
0
1000
2000
3000
4000
Fimi Yasa
Gemena Fimi
Kuno Luiza
Lexi Kuno
Luiza Gemena
Yasa Lexi
Fraukje Sandra
Kara Fraukje
Kofi Kara
Lobo Kofi
Lome Lobo
Sandra Lome
Bonobos
Chimps

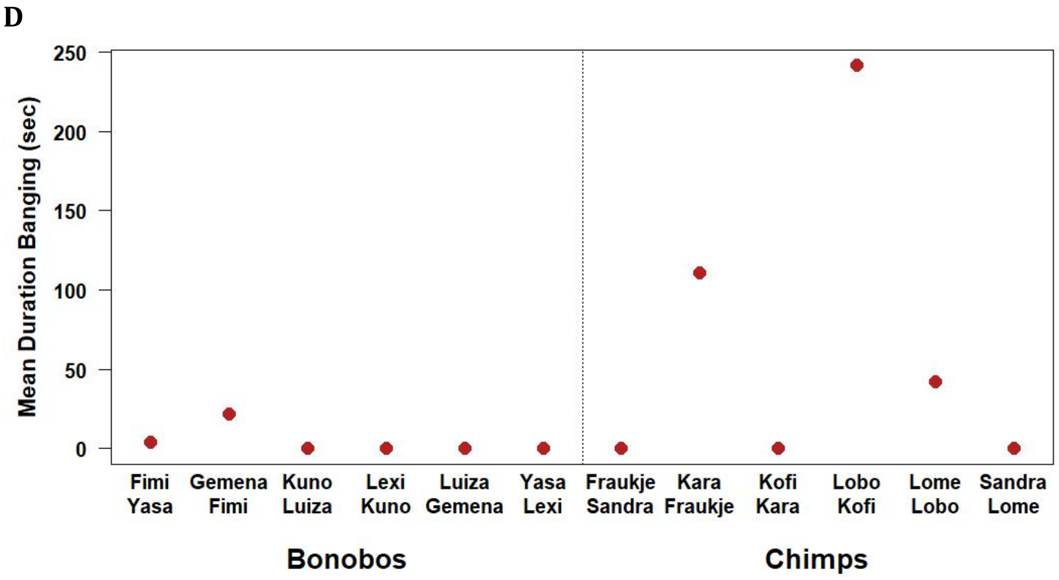


Figure 2.9 Mean duration of scratching (A), reaching (B), staying in close proximity (C), and banging (D) that was exhibited by the six receivers of both species in experiment 'Helping 1'. The receiver of each pair is listed above the helper. Pair "Fimi-Yasa" and "Kara-Fraukje" are the mother-daughter dyads. Pair "Lome-Lobo" are maternal male siblings.

Table 2.4 Results of the GLMM that assessed whether the variable species influenced the likelihood that recipients scratched themselves.

Term	Estimate	SE	lower CI	upper CI	χ^2	*P*
Intercept	-0.74	0.32	-1.42	-0.09	(3)	(3)
Species Chimp vs Bonobo	1.23	0.39	0.42	2.07	7.47(2)	.006(2)
Session(1)	0.07	0.15	-0.23	0.39	0.23(2)	.631(2)
Condition					27.67(2)	<.001(2)
Same vs Control	1.87	0.37	1.14	2.72	(3)	(3)
Different vs Control	1.67	0.40	0.91	2.63	(3)	(3)
Age Helper(1)	0.47	0.31	-0.16	1.13	(3)	(3)
Age Receiver(1)	0.33	0.32	-0.31	1.04	(3)	(3)
Interaction(1)						
Age Helper*Age Receiver	0.89	0.46	-0.02	1.9	3.66(2)	.056(2)

(1) standardized to its mean
(2) overall effect of the predictor
(3) not shown because of limited interpretation

Table 2.5 Results of the GLMM that assessed whether the variable species influenced the likelihood that recipients reached through the mesh connecting the two cages.

Term	Estimate	SE	lower CI	upper CI	χ^2	*P*
Intercept	-3.85	0.87	-5.98	-2.26	(3)	(3)
Species Chimp vs Bonobo	-1.79	1.01	-4.02	0.44	2.67(2)	.102(2)
Session(1)	-0.09	0.23	-0.57	0.46	0.14(2)	.705(2)
Condition					13.13(2)	.001(2)
Same vs Control	1.82	0.73	0.09	14.27	(3)	(3)
Different vs Control	2.27	0.54	0.1	3.64	(3)	(3)
Age Helper(1)	0.99	0.85	-1.47	2.74	(3)	(3)
Age Receiver(1)	-1.69	0.82	-3.72	-0.09	(3)	(3)
Interaction(1)						
Age Helper*Age Receiver	0.62	1.29	-3.52	3.19	0.20(2)	.653(2)

(1) standardized to its mean

(2) overall effect of the predictor

(3) not shown because of limited interpretation

Table 2.6 Results of the GLMM that assessed whether the variable species influenced the likelihood that recipients stayed in close proximity to the helper.

Term	Estimate	SE	lower CI	upper CI	χ^2	*P*
Intercept	2.01	0.67	0.65	3.45	(3)	(3)
Species Chimp vs Bonobo	0.10	0.85	-1.72	1.90	0.01(2)	.905(2)
Session(1)	-0.56	0.18	-0.93	-0.21	9.39(2)	.002(2)
Condition					0.64(2)	.726(2)
Same vs Control	0.31	0.48	-0.55	1.53	(3)	(3)
Different vs Control	0.33	0.56	-0.52	1.92	(3)	(3)
Age Helper(1)	1.70	0.68	0.37	3.18	(3)	(3)
Age Receiver(1)	-2.14	0.67	-3.61	-0.77	(3)	(3)
Interaction(1)						
Age Helper*Age Receiver	1.06	0.76	-0.54	2.65	1.83(2)	.176(2)

(1) standardized to its mean

(2) overall effect of the predictor

(3) not shown because of limited interpretation

Table 2.7 Results of the GLMM that assessed whether the variable species influenced the likelihood that recipients banged against the mesh.

Term	Estimate	SE	lower CI	upper CI	χ^2	*P*
Intercept	-79.10	117.16	-105.95	-47.7	(3)	(3)
Species Chimp vs Bonobo	12.25	78.89	-16.50	44.68	1.78(2)	.184(2)
Session(1)	-8.87	10.24	-14.47	4.64	5.42(2)	.02(2)
Condition					11.86(2)	.003(2)
Same vs Control	25.5	50.33	-14.47	4.64	(3)	(3)
Different vs Control	28.75	50.15	-2.62	38.52	(3)	(3)
Age Helper(1)	1.25	70.38	-1.21	35.92	(3)	(3)
Age Receiver(1)	-4.82	107.22	-38.84	5.11	(3)	(3)
Interaction(1)						
Age Helper*Age Receiver	11.30	127.07	-1.65	46.7	-17.44(2)	1.00(2)

(1) standardized to its mean
(2) overall effect of the predictor
(3) not shown because of limited interpretation

Additionally, we assessed whether the behaviour of bonobo receivers differed before and after they received the correct tool. This deepens our understanding of why the receivers behaved in the observed manner and rules out the possibility that, for example, reaching and transfers merely coincided in a given session but did not precede each other. Bonobo receivers reached in 60% of the sessions before obtaining the necessary tool but they continued reaching only in 10% of the sessions afterwards. Comparing the GLMM that included the key predictor 'before versus after' and its interaction with the type of behaviour with a model only comprised of the factor behaviour, the control factors, and random intercepts and slopes showed that the predictors together significantly contributed to explaining whether a transfer occurred, $p < .001$ ($\chi^2 = 22.31$, $df = 3$, $N = 696$; see Table 2.8). The interaction between the effect of 'before versus after' and the type of behaviour executed by the receiver was highly significant ($\chi^2 = 16.68$, $df = 2$, $p < .001$). This indicates that the degree of change in the likelihood of the receiver executing the behaviour before versus after the correct transfer occurred was significantly different between at least two of the behaviour types. Bonobos stayed in close proximity to a similar degree before and after they received the correct tool (Figure 2.10). However, they scratched themselves less after the correct transfer occurred. The largest difference concerns reaching: Figure 2.10 shows that receivers exhibited substantially less reaching after they obtained the correct tool.

Table 2.8 Results of GLMM that assessed what variables influence the occurrence of recipient's behaviours before and after the correct tool is transferred by the helper. Parametric bootstrap confidence intervals used.

Term	Estimate	SE	lower CI	upper CI	*Z*	*P*
Intercept	5.77	1.02	4.48	27.06	(3)	(3)
Before vs After	-1.34	0.92	-5.98	5.84	(3)	(3)
Behaviour Type						
Reaching vs Close Proximity	-9.26	1.23	-44.23	-7.89	(3)	(3)
Scratching vs Close Proximity	-6.85	1.09	-38.78	-5.44	(3)	(3)
Interaction						
Before vs After*Behaviour Type					16.68(2)	<.001(2)
Reaching vs Close Proximity	6.25	1.37	4.18	28.51	(3)	(3)
Scratching vs Close Proximity	3.32	0.97	0.70	18.36	(3)	(3)
Condition Same vs Different	0.11	0.26	-0.99	1.51	0.17(2)	.685(2)
Session(1)	-0.40	0.17	-3.63	-0.06	4.51(2)	.034(2)
Experiment					0.64(2)	.725(2)
Helping 1 vs Cooperation	0.23	0.50	-2.31	2.93	(3)	(3)
Helping 2 vs Cooperation	0.39	0.63	-0.97	7.82	(3)	(3)
Age Helper(1)	0.43	0.22	-0.03	4.97	(3)	(3)
Age Receiver(1)	-2.83	0.90	-19.41	-1.15	(3)	(3)
Interaction(1)						
Age Helper*Age Receiver	4.39	1.56	1.55	29.27	2.47(2)	.116(2)

(1) standardized to its mean
(2) overall effect of the predictor
(3) not shown because of limited interpretation

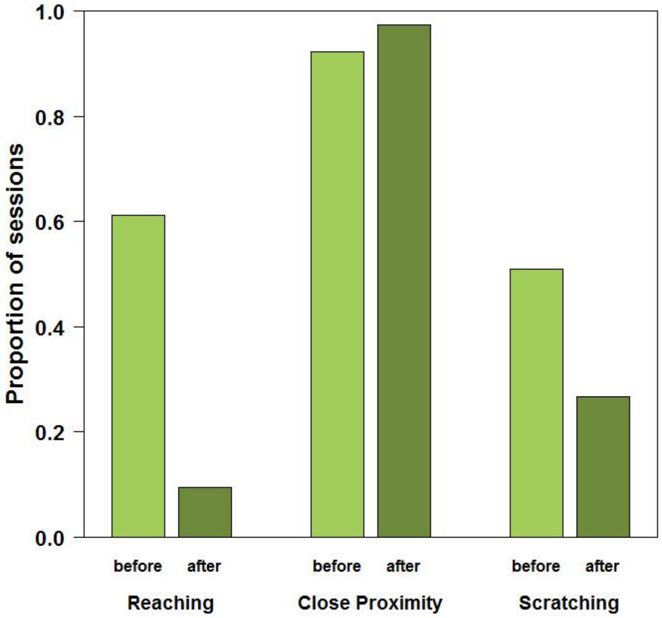


Figure 2.10 Proportion of sessions in which the receivers were reaching, staying in close proximity, and scratching before and after the correct tool was shared while controlling for the influence of the other predictors in the model.

We fitted an additional model, which investigated whether the behaviours occurred before versus after the first incorrect tool was shared in a session. This allowed us to understand whether in the previous model the effect of 'before versus after' was merely apparent because any tool instead of the correct one was shared. Comparing the new model with the respective model from which the main effect of 'before versus after' and its interaction term with the type of behaviour was omitted, yielded a nonsignificant result (χ^2 = 6.75, *df* = 3, *N* = 552, *p* = .080; see Table 2.9). Therefore, the predictor and interaction term did not significantly contribute to explaining why behaviours were executed by the receivers in case an incorrect tool was shared. We thus conclude that the effect of 'before and after' was contingent on whether the correct tool was shared and not just any tool.

Table 2.9 Results of GLMM that assessed what variables influence the occurrence of recipient's behaviours before and after the incorrect tool is transferred by the helper. Parametric bootstrap confidence intervals used.

Term	Estimate	SE	lower CI	upper CI	*Z*	*P*
Intercept	2.93	0.77	1.69	15.07	(3)	(3)
Behaviour Type						
Reaching vs Close Proximity	-5.67	0.96	-31.28	-4.14	(3)	(3)
Scratching vs Close Proximity	-4.35	0.98	-24.07	-2.79	(3)	(3)
Before vs After	1.13	0.90	-0.85	7.60	(3)	(3)
Interaction						
Before vs After*Behaviour Type					2.27(2)	.321(2)
Reaching vs Close Proximity	1.40	1.16	-3.38	12.34	(3)	(3)
Scratching vs Close Proximity	0.94	0.92	-2.40	10.42	(3)	(3)
Condition Same vs Different	-0.25	0.41	-1.87	1.03	0.32(2)	.57(2)
Session(1)	-0.33	0.15	-2.21	0.02	3.88(2)	.049(2)
Experiment					3.68(2)	.159(2)
Helping 1 vs Cooperation	0.12	0.45	-1.07	3.64	(3)	(3)
Helping 2 vs Cooperation	0.7	0.35	-0.08	6.41	(3)	(3)
Age Helper(1)	-0.06	0.19	-0.80	1.01	(3)	(3)
Age Receiver(1)	-0.04	0.65	-3.69	3.22	(3)	(3)
Interaction(1)						
Age Helper*Age Receiver	-0.55	1.12	-8.24	3.32	1.46(2)	.228(2)

(1) standardized to its mean
(2) overall effect of the predictor
(3) not shown because of limited interpretation

3. How did the helper select the tools?

Comparing the GLMM that included the key predictors experiment, condition, and type of tool the receiver needed with a model from which these variables were omitted showed that the predictors together are not significantly contributing to explain whether the correct tool was transferred first ($\chi^2 = 3.4$, df = 4, N = 135, p = .494; see Table 2.10). Therefore, even though helpers benefitted from transferring the correct tool in experiment 'Cooperation' they did not pay more attention to the needs of the receiver than when they did not benefit from such transfers. It also did not make an obvious difference if helpers needed to share the same tool as the one they had to use themselves (condition 'Same') or a different tool than the own (condition 'Different'). Finally, helpers also did not prefer to share one specific type of tool. However, the factor tool type was somewhat unstable in this model (orig. = 1.06, min. = 0.13, max. = 1.65) and interpreting this finding has to be done with caution.

Since the predictors of this model were did not significantly contribute to explain when a correct tool was transferred first, we ran two separate models. In the first, condition 'Same' was the reference group and in the second, condition 'Different' was the reference group while keeping all other predictors centered. Testing the intercept of the first model against a chance level of 2/3 showed a nonsignificant difference from chance, *p* = .096. Testing the intercept of the second model against a chance level of 1/3 also showed a nonsignificant difference from chance, *p* = .315. Therefore, it did not matter if receivers needed the same or a different tool than the helper, in both scenarios the helper seemingly transferred tools randomly.

Table 2.10 Results of GLMM that assessed whether the correct tool was transferred first.

Term	Estimate	SE	lower CI	upper CI	*Z*	*P*
Intercept	-1.17	0.60	-2.59	0.19	*	*
Experiment						
Helping 1 vs Cooperation	0.37	0.51	-0.86	1.42	0.73	.463
Helping 2 vs Cooperation	0.65	0.46	-0.26	1.80	1.44	.151
Condition						
Same vs Different	-0.04	0.38	-0.80	0.92	-0.11	.914
Tool type receiver needs						
Stick vs Block	1.06	0.94	-1.35	3.60	1.14	.256
Session	0.08	0.20	-0.59	0.52	0.38	.702
Age Helper	-0.33	0.22	-0.8	0.17	-1.49	.137

(1) standardized to its mean
(2) overall effect of the predictor
(3) not shown because of limited interpretation

D. Discussion

While we found spontaneous tool transfers in all female-female bonobo dyads even when they did not directly benefit from it, only two transfers occurred in the mother-daughter chimpanzee dyad. Once bonobo helpers benefitted from tool transfers and understood the task, they shared tools consistently. In contrast, none of the chimpanzee helpers shared a tool in the cooperative task even though they would have gained rewards through it. To control for the influence of gaining more experience over time, we switched back to the helping task for all dyads that shared tools in the cooperative task. While bonobos continued to share tools at a high rate, they did so randomly dispersed across sessions instead of consistently as in the cooperative task. Across experiments, transfers occurred when there was a need for it and not just because another individual was present. Begging influenced the likelihood that tools were shared by bonobo helpers. Nevertheless, both species begged to a similar degree. Receivers exhibited begging significantly less often once they acquired the correct tool. We did not find evidence that helpers tailored the tool selection to the need of the receiver but randomly transferred tools until the correct one was transferred.

Only one of the six chimpanzee helpers transferred a single tool to her subadult daughter in two sessions of the helping task and none of the six helpers transferred any tool in the cooperative task. There might be two possible explanations, one for each experiment, why chimpanzees did not transfer tools in this study. When contrasting our findings from the *helping task* with previous research, which did observe that chimpanzees transfer objects (e.g. Yamamoto et al., 2009, 2012), one difference seems to be that in such studies helpers did not receive any other task than transferring objects. In our study, helpers could operate their own apparatus and acquire rewards themselves. They were therefore not confronted with the alternative of either transferring an object or doing nothing. As was discussed, Tennie and colleagues (2016) found that chimpanzees released a peg that was holding a baited apparatus out of reach from the conspecific at the same rates independent of whether the result helped or hindered the partner access the food. This calls into question why chimpanzees performed the behaviours observed in helping studies. In both their and the original study (Melis et al., 2011), chimpanzees received a towel soaked in juice and a non-functional rope as distractor items in order to decrease manipulation rates by the subjects and prevent ceiling effects. Already Melis and colleagues (2011) reported lower response rates (50–55%) in their study compared to previous studies without distractor items by Warneken et al. (75%, 2007) and Yamamoto et al. (80%, 2009). In our study subjects could retrieve rewards by operating their own apparatus, which was not only a distractor item but a goal-directed task. This might have further decreased response rates that were not prosocially motivated. To tease apart whether this explanation holds true, controlled experiments are needed that not only vary the outcome of the partner but also the degree of involvement in distractor tasks given to the subject.

In the *cooperative task* chimpanzees would have benefitted from transferring a tool, but we still did not observe a single transfer. One explanation could be that helpers did not share tools because they might have perceived the task as competitive rather than cooperative. Each individual only completed a non-social training, in which they could access both sides of the apparatuses and subsequently eat all grapes. In the test, chimpanzees might have misperceived the task and expected that all grapes are distributed to the individual that is fastest. This could have prevented them from recognizing that the partner did not have a tool. Nevertheless, during the control condition helpers had the chance to perceive the contingencies of the apparatus and that the rewards were evenly distributed. Yet, apes received the control condition only on one out of three trials per testing day, which might have been not enough experience. To assess and rule out the possibility that chimpanzees perceived the task as competitive, future studies could incorporate a social training for half the sample and in the end compare both groups.

In comparison to the negligible frequency of transfers done by chimpanzee helpers, we found that female bonobos shared tools with their female partners even when they did not directly benefit. The male bonobo did not transfer any tool to his female partner in either experiment, nor did the female helper share a tool with him. Even though this result is intriguing and might further point to the notion that mainly female bonobos cooperate and support each other, our sample size is too small to draw definite conclusions as the effect might be influenced by this particular male. Large scale studies including more mixed-sex and additionally male-male dyads are needed to assess if our result holds true. Bonobo helpers that did transfer tools were sensitive to whether a tool was needed by the receiver and did not transfer tools merely because a partner was present. Still, they did not transfer the correct tool first. Transferring several tools in a session came at no direct cost (as we provided spare tools and none was useful after retrieving the own rewards). This could have decreased the pressure to keep track of which tool exactly was needed by the partner. A follow-up experiment, in which the helpers are forced to decide between both tool types instead of having access to all, could be used to answer this question. When bonobo helpers did not benefit from tool transfers the probability of a transfer did not increase over the course of the experiment and transfers were randomly dispersed over the twelve sessions. However, when they did benefit in the cooperative task they transferred tools in every session once they learned how the task works, revealing motivational differences between the two experiments.

Bonobo receivers reached less often after they received the correct tool and this drop was contingent on whether the correct tool was shared and not just any tool. Even though the individual was occupied with retrieving the food and consuming it upon receiving the correct tool, in most cases there was still enough time left to continue begging. We also wanted to rule out the possibility that receivers were just reaching to acquire any tool and did not specifically request the correct one. The likelihood that bonobo helpers shared a tool was in fact significantly influenced by the reaching of receivers. This finding did not hold true for chimpanzees, given that we did not find species differences in the duration of reaching. However, bigger samples are needed to make definite claims. The sharing-under-pressure hypothesis suggests that food or object sharing in apes can be explained by requests and resulting harassment of the partner and not due to a prosocial motivation (Stevens, 2004). If one assumes that sticking the fingers through the mesh is influencing the partner with such intensity to consider it harassment, this could explain the occurrence of transfers by bonobo helpers but not the lack of transfers by chimpanzee helpers.

One explanation might be that the two species are differently susceptible to the influence of harassment. An alternative explanation might be that bonobos are better able to interpret such behaviours, possibly due to enhanced empathetic abilities. As was discussed above, bonobos seem more adept at processing socially relevant stimuli (Clay et al., 2016; Herrmann et al., 2010; Kano et al., 2015; Rilling et al., 2012) and could have benefitted from their possibly heightened awareness of their partners' needs in our study. Either of these explanations might have helped bonobos to understand the cooperative task more easily than chimpanzees. We found lower rates of transfers in the first than second helping task, which could suggest that bonobo helpers learned to better interpret the reaching behaviour of their conspecifics during the cooperative task. Through this, they were either able to act more prosocially or were more susceptible to harassment in the second helping task than in the first.

In chimpanzees we would expect males to be most likely to cooperate with one another (Pusey & Schroepfer-Walker, 2013). Both tested chimpanzee male-male dyads were composed of males that had strong positive bonds at the time of the study. One pair was composed of full brothers who supported each other during fights while one rose to the position of the alpha male. The other pair was composed of two males of the same age that grew up together and, at the time of the study, played together fairly often. Moreover, for each species we incorporated one dyad that was composed of a female and her daughter. Therefore, we do not think that the relationship-quality of chimpanzee and bonobo dyads greatly different to each other. However, due to logistical reasons we are lacking data to support this claim. Our sample size would have been too small to draw accurate conclusions with regard of the influence of social relationship of each dyad on the likelihood that the helper shared a tool. Future studies should include measures of relationship quality whenever possible and in case the sample size is large enough to accurately use such measures. Tolerance constraints, if it is seen as not wanting to be physically close to the partner, should not influence our results to a great extent given that conspecifics were separated by mesh and tools could be passed into the other's cage without necessarily being in close proximity to the partner.

Even though bonobos could have also shared the food they acquired themselves in the helping task, they never did so and only transferred tools. Previous studies only observed bonobos to transfer food instead of objects (Hare & Yamamoto, 2017; Krupenye, Tan, & Hare, 2018), so this is the first study to show that bonobos also transfer objects in order to help a conspecific. In comparison to Krupenye and colleagues (2018), bonobos of our study could retrieve food that is easily consumed without any preceding processing. Nevertheless, it would have been possible for the helpers to respond to their partner's begging by transferring grapes as well. We think the most likely reason of why bonobos transferred tools but not food in our study is that this way they were able to maximize benefits for themselves and their partner. If they would have only transferred grapes, they would have lost their food while their partner's food remained inaccessible. Only by retrieving and consuming the own food and transferring a tool to their partner could both benefit. This is the most salient difference to the study by Krupenye and colleagues (2018) and future studies could make an effort to combine the two designs in order to clarify possible explanations.

We found that bonobos outperformed chimpanzees on both an altruistic and a cooperative task. The ability to perceive situations as cooperative and understand that a mutual benefit can result from them, is essential to support cumulative cultural evolution. Altruistic and cooperative exchanges allow for more frequent and possibly more tolerant interactions, which in turn increase the chance for observing and socially learning skills or rare innovations (Hill et al., 2011). Moreover, teaching has been classified as a form of altruism as the teacher provides knowledge or induces a new behaviour that is immediately or ultimately beneficial for the trainee (Fogarty et al., 2011; Tennie et al., 2009). In such social structures, the costs of complex social learning mechanisms become outweighed by the benefits and result in an accumulation of more complex cultural traditions (Hill et al., 2011). Thus, in humans, cumulative culture might have been made possible through the development of regulated cooperative exchanges and the reinforcement of altruistic responses (Hill et al., 2011). Given that bonobos seem better able to understand when situations call for cooperation and when a partner is in need of help, they might be a possible candidate species to test whether they might show cumulative improvement of behaviours displayed in the wild or captivity. Chimpanzees are well-known for their tool use and manufacturing behaviour, and it is currently unknown whether they transmit such knowledge to others or cumulatively adapt skills (refer to Chapter 1, section 3; and Chapter 3). Bonobos in comparison do not use tools in the wild and seem like the less likely species to show cumulative culture. However, as I discussed in chapter 1 section 1, two different research teams found that nonhuman species (i.e. ungulate species and pigeons) were able to build on the knowledge of previous generations during spacial navigation. Those results highlight the importance of considering other domains, in which populations might accumulate knowledge cumulatively. Instead of focusing on technological advances such as tool manufacture, potential relevant domains to understand whether bonobos show cumulative culture might be spacial navigation, communication systems, or foraging strategies.

The results of this study underline the fact that we need to directly compare bonobos and chimpanzees and use the same design for both species if we want to understand which factors influence the expression of prosocial behaviours and to better understand the evolution of human cooperation and consequently human cumulative culture.

III. Chapter 3: Teaching in chimpanzees

A. Introduction

Chimpanzees are capable tool users and have been found to show cultural variation on several different types of behaviours (Whiten et al., 1999). Even though they tend to be conservative when solutions to a task still produce a reward, chimpanzees are able to inhibit these responses and switch to new solutions once the old ones become obsolete (Manrique et al., 2013). Furthermore, they are able to socially learn new behaviours through emulation and possibly imitation (Buttelmann et al., 2007; Call et al., 2005; Hopper et al., 2008; Horner & Whiten, 2005). Thus, innovative behaviours can be socially transmitted with high fidelity. One of the big questions that is currently unanswered is whether chimpanzees teach. Researchers are trying to investigate whether cultural variation between chimpanzee groups is not only supported by efficient social learning strategies but also by active teaching on the part of the knowledgeable individuals. For example, do chimpanzee mothers actively facilitate learning in their youngsters or do these have to rely solely on close observation?

To understand whether chimpanzees have the cognitive capacities to support teaching, we can apply the mentalistic approach as described in Chapter 1 (section B3; p. 14). Advocates of the mentalistic approach argued that in order to teach the actor needs to have the cognitive capacity to form a theory of mind (Kruger & Tomasello, 1996), to plan into the future (Vale et al., 2012), and the intent to teach as stated by the given working definition of teaching. Recent evidence by Krupenye, Kano, Hirata, Call, and Tomasello (2016, 2017) revealed that chimpanzees have at least a rudimentary theory of mind and can anticipate the actions of observed agents while incorporating their false belief. Additionally, they are able to understand the goal of an agent and mistakes made while trying to achieve that goal (Call et al., 2005). Furthermore, when facing a threat such as snakes, wild chimpanzees emit alarm calls in the presence of ignorant group members (Crockford, Wittig, Mundry, & Zuberbühler, 2012). These different lines of studies suggest that chimpanzees can form a representation of ignorance in others and that they understand when another individual holds a wrong belief about situations or when another individual performs actions that are inadequate to achieve a goal. At least when facing snakes, they are also willing to inform others of such potential danger. Finally, different studies and observations showed that chimpanzees save and produce tools for future use (Bräuer & Call, 2015; Osvath & Karvonen, 2012; Osvath & Osvath, 2008) and, thus, are able to use foresight. Therefore, chimpanzees might either not be motivated (i.e. do not intend) to teach, or they might be lacking a full-blown theory of mind that is needed to identify the zone of proximal development of another individual (Vygotsky, 1978). The age of three to five years seems to be a critical window for chimpanzee infants during which they need to sufficiently learn tool techniques (Matsuzawa, 1994). Considering that chimpanzee females give birth on average every five years until the current infant is independent enough to sustain itself more readily (Matsuzawa, 2011), such high costs of parental investment pose a sufficiently strong incentive for chimpanzee mothers to ensure that their young will adequately learn all necessary skills before the end of their critical learning period. Therefore, at least chimpanzee mothers might be motivated to teach their young.

Evidence regarding teaching in wild populations has been scarce so far and difficult to obtain because closely observing chimpanzees in their natural environment is generally difficult and clearly distinguishing teaching instances from other forms of social interactions becomes challenging. Boesch (1991) was the first to claim that he observed teaching instances between two chimpanzee mothers and her infants at Taï forest, Ivory Coast (for detailed descriptions refer to Chapter 1, section B3; p. 14). However, these interactions were not video recorded to further analyse them, and until now no detailed assessment was made whether other mothers at Taï might actively facilitate learning in their offspring. At other field sites, research teams that conducted long-term experiments to assess skill acquisition by chimpanzee infants reported that they did not observe a single interaction between mothers and their young that could be classified as active teaching (Lonsdorf, 2006; Matsuzawa et al., 2001). For example, in 13 years of research Matsuzawa and his colleagues (2001, 2011) never observed any instances in which mothers actively modified their infants' grip or position of tools. Nor did they observe instances in which mothers directly handed specific tools or nuts to their infants.

Recently, an intriguing finding was published by Musgrave and colleagues (2016). They report that mothers provided sticks to their young while termite fishing at a field site located at the Goualougo Triangle, Nouabalé-Ndoki National Park, Republic of Congo. The research team observed stick transfers to infants in 13 unique dyads, 12 from mothers and one from the sub-adult sister. They state that transfers observed in these 13 dyads fulfil the three criteria to identify teaching as proposed in the functionalistic approach by Caro and Hauser (1992; for details refer to Chapter 1, section B3; p. 14). The adults modify their behaviour in the presence of the young (i.e. transfer a tool), they incur a cost by such transfers (i.e. reduced food intake), and young supposedly learned through such higher rates of opportunities (i.e. the amount of insertions and feeding increased after transfers). While this finding is extremely valuable not only for assessing teaching but also for developing a better understanding of targeted helping, more evidence is needed in order to clearly classify the observed behaviour as teaching. As Thornton and Raihani (2010) stated, in addition to the second criterion put forward by Caro and Hauser (1992) - a cost or no immediate benefit to the teacher - no other alternative primary function of the given teaching instance should be apparent. Thus, evidence is required that the specific behaviour was selected to facilitate learning and not to primarily support another function, such as providing nutrition. Given that termites cannot be acquired without a tool, transfers might have the primary function to provide nutrition instead of facilitating learning. An even lower alternative explanation in terms of social cognition would be that mothers bring additional tools or hand over their tools to stop the infant from harassing them. In case it is possible to show that adults adapt the rate or style of transfers to the age or knowledge state of infants, this would constitute evidence in favour of the behaviour being classified as teaching. Additionally, we would need evidence that active transfers, rather than picking up discarded tools, are actually enhancing infants' ability to fish termites (i.e. that they learn more efficiently upon receiving a tool directly from others). Such findings would support the notion that adults provide opportunities to learn instead of help their young access food. Elaborating on this finding could thus be worthwhile.

Studying teaching behaviour in more controlled experimental set-ups so far also yielded mostly negative results. Povinelli and O'Neill (2000) adapted a dyadic box-pulling task, which was originally used by Crawford (1937) to study cooperation. In the original experiment, both chimpanzees of a dyad were trained to jointly pull at a string in order to drag a heavy box within reach. Povinelli and O'Neill (2000) adapted this design and only trained one chimpanzee of a dyad and assessed whether these experienced chimpanzees would solicit the naïve partner’s attention or instruct the partner in how to solve the task. The researchers argued that behaviours such as pointing toward aspects of the task, showing the action, or physically leading the partner to the correct location might be used by experienced chimpanzees to direct their naïve partners. Some of these behaviours were recorded by Crawford (1937), who for example observed that chimpanzees would engage the partner by walking over and guiding him or her back to the task through touches. However, the chimpanzees in Crawford’s experiment were all familiar with the task, and the behaviours only appeared relatively late during the experiment. This might point to a ritualization instead of spontaneous application and, thus, no explicit understanding of the effect of such behaviours (Povinelli & O’Neill, 2000). Povinelli and O'Neill (2000) therefore decided to minimally train the chimpanzees that subsequently acted as experienced subjects. They found that while the two experienced chimpanzees successfully pulled in the box on 83% of trials when working together, they were not successful with any of the five naïve partners except for one individual. After closer inspection, this naïve individual seemed to have picked up the skill by herself instead of being taught by either of the two experienced chimpanzees. The authors did not observe any solicitation gestures or physical guidance in any of the ten unique expert-naïve dyads. Nor did they offer the rope to their naïve partner to elicit pulling. Hirata and Fuwa (2007) reported similar findings in a non-teaching context. They elegantly modified Crawford’s apparatus so that the rope comes loose if only one chimpanzee pulls it (refer to chapter 2 for more details on the loose-string task). This modification ensured that chimpanzees have to synchronize their actions with that of their partner or else risk failing the task. Consequently, increased communication might be the result. Yet, the two tested chimpanzees never established mutual eye contact and did not solicit each other or interact in any other relevant manner. Only when paired with a human partner, one of the two chimpanzees started to use solicitation gestures to recruit his help. This behaviour immediately ceased once the same chimpanzee was again paired with her conspecific. The authors argued that the expert chimpanzee had learned from previous interactions that "it was fruitless to show soliciting behaviour to [a conspecific], whereas it worked with humans" (p. 20). Though the difference between communication when facing a conspecific and human partner is interesting, we need to be careful in interpreting its reliability as the sample size is one of only two tested individuals.

A second negative result in regard to teaching was provided by Dean and colleagues (2012), who showed that children used teaching to transmit knowledge to their partner about an apparatus, but chimpanzees did not. The researchers presented chimpanzees and children with a puzzle box that could be solved over three consecutive stages that built upon each other. Thus, if the individuals failed at stage 2 they would not be able to solve stage 3. The puzzle box was introduced in an entire group of subjects (chimpanzees: four groups; children: eight groups) to assess the spread of knowledge and allow for a more naturalistic occurrence of teaching, cooperation, and learning. Furthermore, in a second experiment the researchers trained one chimpanzee in each of four additional groups to solve all three stages of the puzzle box. Instances of direct teaching were observed in all groups of children, which involved instructive verbal communication. In about a third of such instances, children additionally used gestures. In contrast, none of the interactions performed by chimpanzees tested in both experiments could be classified as teaching.

Only Grosse, Call, Carpenter, and Tomasello (2015) found that chimpanzees would demonstrate relevant actions to a seemingly unable human partner. The researchers installed two empty apparatuses inside the apes' cage and placed a baited duplicate of either two outside the cage. A human partner operated that baited apparatus in an unsuccessful manner while gaze alternating between the ape and the apparatus. In case the ape manipulated the corresponding empty apparatus in a correct manner, the human partner replicated the actions on the own apparatus and handed the rewards to the ape. The research team showed that children placed in such a situation started to use gestures to demonstrate the correct motions that the partner had to perform in order to retrieve the reward. In contrast, chimpanzees did not use gestures to instruct the human partner. However, at least for one of the two apparatuses they manipulated the corresponding empty apparatus significantly more often in a correct manner than the second apparatus if the rewards were located inside the partner's apparatus versus outside on the table. In the latter scenario, demonstrating the correct actions is obsolete as the human did not have to retrieve the rewards from the apparatus. Even though this behaviour does not fulfil the second criterion of Caro and Hauser's (1992) functional definition (a cost or no immediate benefit to the teacher), it is the only compelling evidence so far that chimpanzees might be able and willing due to self-interests to demonstrate an action to a naïve partner.

With regard to bonobos, Savage-Rumbaugh, Rumbaugh, and McDonald (1985) observed the bonobo Kanzi to spontaneously invent iconic gestures that he possibly used to request an action of the human partner. Some of these gestures were twisting and hitting motions to request help in opening jars or cracking nuts. Since these gestures represent the actual motions that have to be performed on the object, they could be seen as instructing the partner in how to reach the outcome. Nevertheless, Grosse and colleagues (2015) found that zoo-living bonobos would not use gestures or their empty apparatus to instruct a human, and so far no other researchers reported that bonobos used gestures for instructional purposes.

Taken together, evidence for teaching in wild chimpanzee populations is currently limited to anecdotal and preliminary evidence (Boesch, 1991; Musgrave et al., 2016) contrasting decades of an absence of such observations (Lonsdorf, 2006; Matsuzawa et al., 2001). Similarly, researchers conducting experimental studies mainly found negative results (Povinelli & O'Neill, 2000; Dean et al., 2012) and only Grosse and colleagues (2015) found that chimpanzees would instruct a human partner in some contexts. Tennie and colleagues (2009) stated that the absence of teaching could be related to the fact that all behaviours, which have been regarded as chimpanzee traditions, can be easily reinvented by each individual anew. This would render teaching an unnecessary and costly strategy to transmit knowledge that is needed to survive. Other researchers propose that instead of actively demonstrating behaviours, chimpanzees might enhance learning by their young through different means.

Matsuzawa and colleagues (2001) observed that mothers are highly tolerant of their offspring and let them freely interact with the tools, nuts, and products even when this interferes with the task. One-year-old chimpanzees first start to interact with aspects of the nut cracking behaviour by picking up the nuts' kernels once their mother cracked them. While the research team reported that no direct transfers of kernels occurred, mothers often enabled infants to take kernels by continuing to hold them in their hands. Similarly, until the age of three, young chimpanzees are allowed to freely interact with tools, nuts, and kernels of other adult group members. Even though chimpanzees tend to be somewhat intolerant towards adult group members while nut cracking, such tolerance towards infants allows them to be physically close and observe the task at hand more effectively (Matsuzawa et al., 2001). This results in ample opportunities to interact with and closely observe proficient models throughout the first five years of a chimpanzee's life. Through this, young chimpanzees gain long-term practice while still being taken care of by their mothers. Matsuzawa (2001, 2011) termed this type of interaction between chimpanzee infants and adults the "master-apprenticeship relation" and argued that no active teaching is needed as it sufficiently enables young chimpanzees to learn all necessary skills.

Along the same lines, Moore (2013) proposed the term "minimal pedagogy" to account for strategies that do not necessarily involve actively modifying the own motions while demonstrating (e.g. slowing down or exaggerating), but rather involves eliciting attention of the naïve individual. Through vocalizations, eye contact, touch, or postural shifts granting visual access mothers could draw the attention of their infants to the task at hand and, thus, enhance their learning efficiency. Such a strategy would only need the actor to form a representation of the other's inability and to perform the action upon recognizing the presence of an intended audience, which both assumingly are within the cognitive capacity of chimpanzees (see discussed above Crockford et al., 2012). In contrast to actively modifying the own motions, such as exaggerating important aspects, minimal pedagogy places no "demands on the ability of teachers to break down and represent to other parts of ordinarily fluid action sequences" (Moore, 2013, p. 897). Direct reports of whether soliciting occurred during feeding contexts are mostly absent and only Lonsdorf (2006) stated that eye contact was rare between mothers and infants.

To sum up, different hypotheses have been put forward that might explain the relative absence of teaching found in chimpanzees. Tennie and colleagues (2009) argue that teaching is not needed as the behavioural repertoire of wild chimpanzees only encompasses skills that are not complex enough for learning through observation to fail. Matsuzawa (2001, 2011) and Moore (2013) on the other hand state that chimpanzees are actually aware of the incompetence of offspring and enhance learning through modifying their behaviour that does not involve active demonstrations. While, Matsuzawa (2001, 2011) suggests that enhanced tolerance towards young chimpanzees provides increased social learning opportunities, Moore (2013) on the other hand proposes that chimpanzees do in fact actively change their behaviour by soliciting the infant's attention or granting visual access through postural shifts. A fourth possibility might be that chimpanzees are in fact modifying their motions while using tools (e.g. slowing down or exaggerating), but in a very subtle manner. Thus, researchers might miss subtle changes in the velocity or style of an action sequence when these are scored by looking at video recordings, especially so when assessing wild populations. Of course we currently do not have the technology to record actions performed by wild chimpanzees in a more controlled manner; however, the laboratory setting allows the usage of a broader range of technological tools that are less prone to miss subtle changes in behaviours. Such subtle changes might be less costly to the actor than moulding the movements of a naïve individual - the actor can for example continue to forage while teaching. Yet, it still enhances learning as slowing or breaking down action sequences grants an easier apprehension of the procedure. As of now, the only evidence that subtle changes might be used during teaching sequences comes from macaques. A population of long-tailed macaques (*Macaca fascicularis*) in Lopburi, Thailand, started to use human hair to floss their teeth (Watanabe et al., 2007). Subsequently, it was discovered that mothers slowed down when flossing their teeth in the presence of their own infants (Masataka, Koda, Urasopon, & Watanabe, 2009). Mothers integrated more pauses during their motions, repeated the actions more often, and each bout within the episode lasted longer when their young were present. It is conceivable that chimpanzees might be able to modify their actions in a similar manner.

In the current study, we therefore used motion trackers that capture even subtle changes in the apes' actions. Such technology has been previously used in studies that for example measure durations of movements during joint actions performed by adult humans (Vesper, Schmitz, & Knoblich, 2017). To understand whether chimpanzees possess the ability to actively teach and which motivational factors govern this, we trained individual chimpanzees to manipulate an apparatus that could be operated by a pulling and subsequent turning motion (the apparatus design was inspired from Call & Tomasello, 1995). These experts were then paired with naïve conspecifics (test condition 'Naïve') and, depending on the experiment, the expert did or did not benefit from passing on their knowledge. In experiment 'Independent', two duplicate apparatuses were mounted to two neighbouring cages, which were separated by mesh. Both apparatuses were baited with rewards and could be operated independently of each other. Thus, the trained individual could retrieve rewards regardless of the skill of the partner. In experiment 'Dependent', however, one apparatus (attached to the cage of the subject's partner) provided rewards to both cages upon successful manipulation, while the second apparatus (attached to the subject's cage) remained empty throughout the entire experiment. Therefore, in order to acquire any rewards, the subject was dependent on the partner successfully operating her apparatus. We included several control conditions. In the control condition 'Empty', no conspecific was present that observed the trained experts. This condition provided a baseline measure of how demonstrators acted in the absence of an audience. In the control condition 'Expert', the partner of the given subject was another trained individual. This condition controlled for the influence of another individual being present and able to access the apparatus instead of being naïve. Finally, in experiment 'Dependent', we included a third control condition to control for the mere presence of a conspecific even though that individual was not able to access the apparatus. Motion trackers attached to either end of the two apparatuses recorded all movements performed by both individuals throughout each session. This enabled us to detect minor changes over the course of the two experiments and between conditions. Moreover, following Moore's approach (2013) we assessed whether solicitation behaviours were exhibited by the subjects or partners. We expected that in case chimpanzees adjusted their behaviour in the presence of a naïve individual such changes would be most pronounced when the subject benefitted from the partner's actions. This study enabled us to further analyse whether chimpanzees might not be observed to teach because they are not motivated to do so due to an absence of direct positive consequences or whether they may lack specific cognitive abilities that could support teaching (e.g. recognizing inability of the partner or being able to modify their own behaviours accordingly).

B. Methods

1. Subjects

Our subjects were six chimpanzees (*Pan troglodytes*, 3 females, 3 males, M_{age} = 16.3 years) housed at the Wolfgang Köhler Primate Research Center at the Zoo Leipzig, Germany. These subjects were paired with naïve partners and additionally acted as expert partners for each other (see Table 3.1). All chimpanzees included in this study participated in cognitive tests done by colleagues, have access to an inside and outside enclosure, and are provided with different types of enrichment every day. Each chimpanzee was mother-reared except for Alex. The apes were never food deprived, and water was also provided ad libitum during tests. Jahaga, Alex, and Daza and their respective partners lived in a social group of seven individuals. Lome, Tai, and Kofi and their respective partners lived in a social group of 18 individuals. Due to time constraints as Jahaga was going to be transferred to another zoo, we started with Jahaga and Alex and once all data was collected we continued with Daza. That way, the data collection of Alex was completed before he again participated as the partner of Daza. The subjects Lome, Tai, and Kofi were tested simultaneously. Daza was the only subject that participated as naïve subject before being tested herself. Daza herself had two different naïve partners, because Jeudi stopped coming into the testing room after her entire data was collected for experiment ‘Dependent’. We had to replace the naïve partners of two other subjects (Jahaga and Kofi) after session four of experiment ‘Independent’ because they continued to destroy the apparatus. After replacing these partners with a new naïve partner we started with session one again. Part of the data collection was done by Anja Hutschenreiter as part of her Master thesis.

Table 3.1 Information about all subjects and their respective partners. Daza first acted as a naïve partner and later as a subject.

Subject & Partners	Sex	Role of Partner	Age	Relatedness	Mother	Father
Jahaga	F	-	23.1	-	Fraukje	Robert
Alexandra*	F	Naïve	16.4	Unrelated	Phil	Tom
Daza	F	Naïve & SF	30.1	Unrelated	Unkown	unkown
Alex	M	Expert	14.9	Unrelated	Agathe	Arthur
Alex	M	-	14.9	-	Agathe	Arthur
Frederike	F	Naïve & SF	42.1	Unrelated	Unkown	unkown
Jahaga	F	Expert	23.1	Unrelated	Fraukje	Robert
Daza	F	-	30.1	-	Unkown	unkown
Jeudi (Exp.2)	F	Naïve & SF	49.9	Unrelated	Unkown	unkown
Hope (Exp.1)	F	Naïve	25.1	Unrelated	Brigitte	Chuck
Alex	M	Expert	14.9	Unrelated	Agathe	Arthur
Lome	M	-	14.7	-	Corrie	Robert
Lobo	M	Naïve	12	Maternal s.	Corrie	Robert
Tai	F	Expert & SF	13.7	Fraternal s.	Riet	Robert
Tai	F	-	13.7	-	Riet	Robert
Sandra	F	Naïve	22.8	Maternal s.	Riet	Robert
Kofi	M	Expert & SF	10.8	Fraternal s.	Ulla	Robert
Kofi	M	-	10.8	-	Ulla	Robert
Bangolo*	M	Naïve	6.8	Unrelated	Dorien	Patrick
Frodo	M	Naïve	22.4	Fraternal s.	Natascha	Robert
Lome	M	Expert & SF	14.7	Fraternal s.	Corrie	Robert

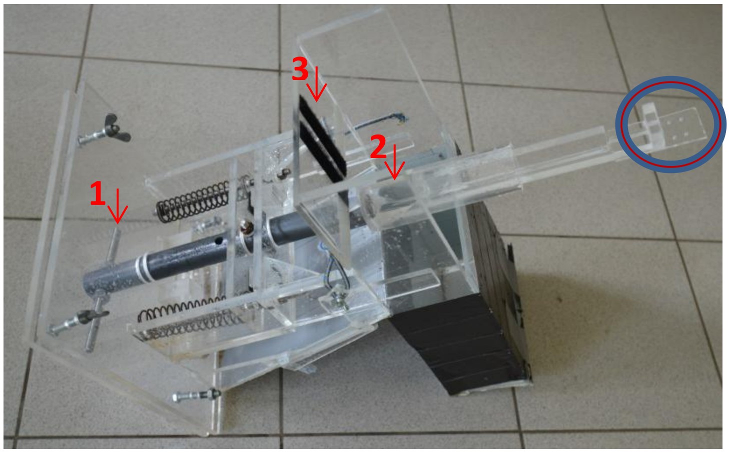
*Individuals that were replaced after four sessions in experiment 1 because they continued to destroy the apparatus.

2. Apparatuses

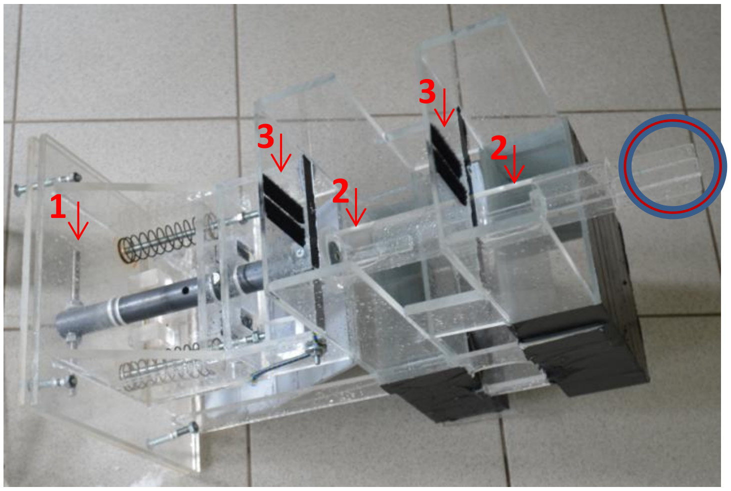
We used three apparatuses that all had the same general mechanism: A handle made out of metal extended into the cage, to which the apparatus was mounted, while the rest of the apparatus remained outside the cage. Chimpanzees could retrieve one "Kinder Surprise Egg" (an egg-shaped plastic capsule) at a time by first pulling and then turning the handle. Each egg contained half a grape as a reward. Ten baited eggs were placed in a tube (hereafter, 'magazine') and attached to the apparatus on top of a rod that connected to the handle. One egg at a time could drop into a round cavity of the rod (see Figure 3.1). To successfully operate the apparatus and retrieve the egg, the ape had to first pull the handle approximately 6.5 to 7.5 cm toward her. Then, while holding it in this position, she had to perform roughly a 100° rotation with the handle, which dropped the egg onto a slide that led to the feeding area. The ape could now retrieve the egg, open it, and consume its contents. If the handle was turned before it was pulled, the egg fell down into a black box attached to the underside of the apparatus and was lost (see Figure 3.1). When the rod was released, it was automatically pushed back to its original position by spiral springs within the apparatus (see Figure 3.1C). Additionally, an elastic band was attached to the rod and stretched whenever the ape turned the handle in either direction (see Figure 3.1C). Once the handle was released the elastic band shrunk again, thereby turning the rod upward. These two mechanisms ensured that the rod was brought back to its original resting position once the ape released the handle from her grip. In case the egg was retrieved or lost, the cavity was now empty and a second egg could drop down from the magazine. In case the egg was not retrieved or lost, the rod slid back to its original position but no second egg could drop down from the magazine. Thus, only one egg could ever be retrieved or lost at a time. We could quickly exchange the magazines once the ten eggs were retrieved or lost, and attach newly filled magazines to the black fabric hook-and-loop fastener (see Figure 3.1).

We used two different versions of the described apparatus. To one apparatus (hereafter 'apparatus single', Figure 3.1A) only one magazine could be attached, and to the second apparatus (hereafter 'apparatus double', Figure 3.1B) two magazines could be attached simultaneously. The mechanism of 'apparatus single' was the same as described above. One magazine was attached to the apparatus and one egg at a time could fall onto the slide and roll towards the operating individual. However, since two instead of one cavity were carved into the rod of 'apparatus double' and two magazines could be attached, the ape could retrieve two eggs simultaneously. One of these eggs fell down onto the slide leading to the operating individual (as for 'apparatus single') and the second egg fell down onto a long slide leading to the adjacent cage. Therefore, operating 'apparatus double' provided simultaneously one egg to the actor and one to the partner in the neighbouring cage.

A



B



C

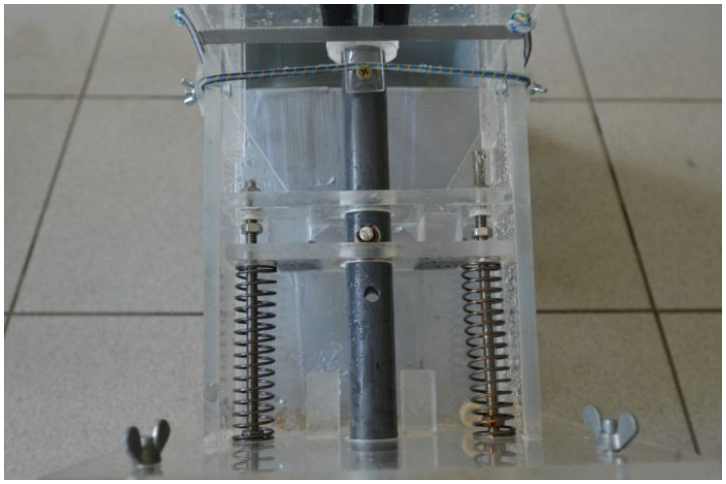


Figure 3.1 Picture of ‘apparatus single’ (A), ‘apparatus double’ (B), and the internal mechanics of either apparatus (C). The handle (marked by a red 1) reached into the cage, while the panel was attached to the mesh. One egg at a time could drop into the cavity of the rod (marked by a red 2). Magazines containing the eggs were attached to the black fabric hook-and-loop fastener (marked by a red 3). We attached the sensors to the end of the rod (marked by blue circles). All measurements of the two apparatuses were the same, including the length from the handle to the place where the sensor was attached.

3. Design

This study entailed two different experiments. In experiment ‘Independent’, teaching did not result in a direct benefit for the subject and in experiment ‘Dependent’ the subject only acquired rewards when the partner successfully operated her own apparatus. Half the sample (Jahaga, Alex, Kofi) started with experiment ‘Independent’ and the other half (Daza, Lome, Tai) started with experiment ‘Dependent’. Both groups subsequently switched to the other experiment, resulting in a within-subject design.

Since the testing facilities were slightly different for the big and the small chimpanzee group, we needed to adapt the set-up for the small group. Chimpanzees of the big group sat in neighbouring cages separated only by a mesh, which allowed for close interactions to occur. Chimpanzees of the small group on the other hand sat in neighbouring cages separated by a booth at the front and a mesh in the back (see Figure 3.2). We used new transparent panels in these cases, so that the visibility into the adjacent cage was maximally enhanced. However, bodily interactions were only possible at the mesh in the back of the cage.

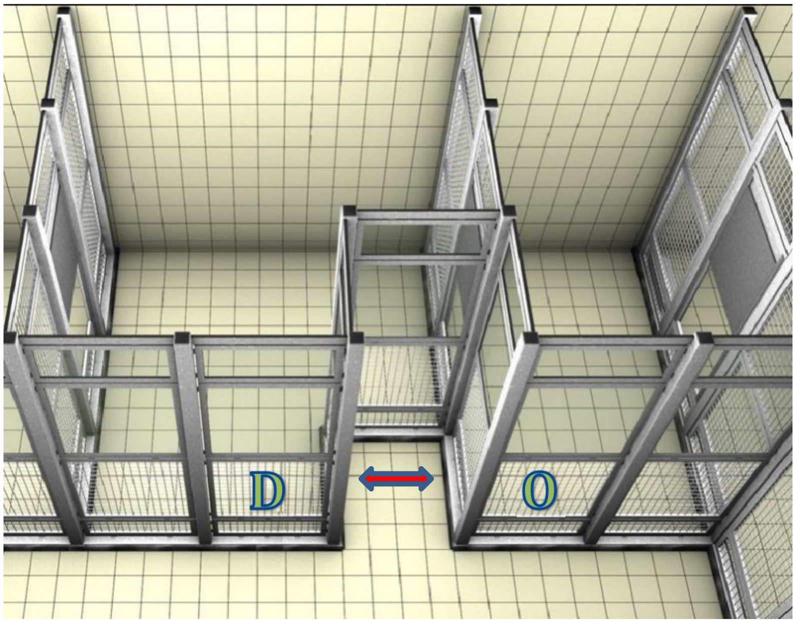


Figure 3.2 Testing room of the small chimpanzee group. The apparatus of the demonstrator was attached to the left mesh next to the booth (D) and the apparatus of the observer to the right mesh next to the booth (O). The sliding door between the two rooms was closed and instead of mesh we used transparent plexiglass at each side of the booth to ensure visibility.

3.1. Training

Depending on which experiment was presented first, the subjects started with either 'apparatus single' or 'apparatus double'. Training was done in three consecutive steps (see Figure 3.3). Each of the three phases of training was the same regardless of which apparatus was used. The only difference was that during training of 'apparatus double' the sliding door between the two cages remained open throughout the session. Thus, the ape was able to freely move between the cages and collect both the rewards distributed to her own and the adjacent cage.

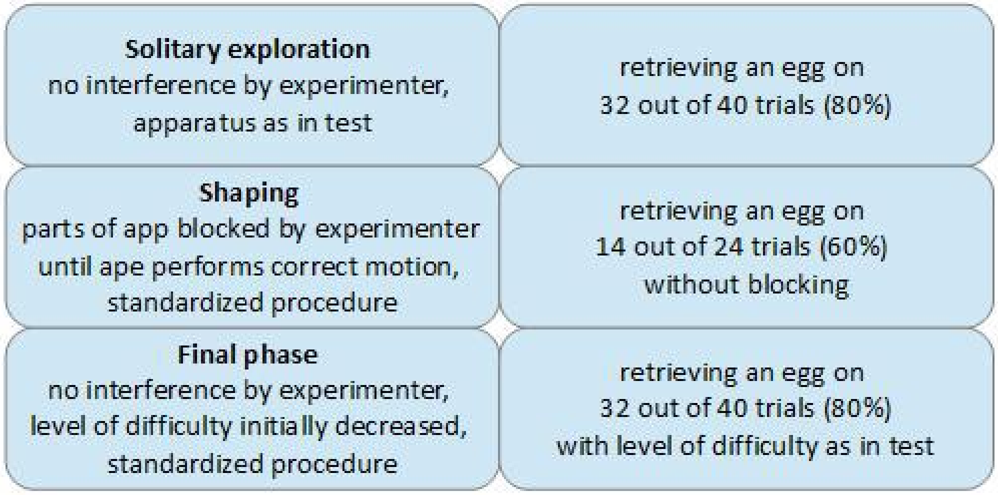


Figure 3.3 Flow-chart of the training regime with criteria for progress to next level.

First, the apes were given a minimum of five and maximum of 15 sessions of *solitary exploration* without any experimenter interference. In each session the ape could retrieve a maximum of 40 eggs, which were contained in four magazines that we attached to the apparatus once the previous magazine was empty (we used a total of 80 eggs for 'apparatus double' since we attached two magazines simultaneously). During these training trials, the individual received no help in finding out how the mechanism worked. That way, we could assess how difficult and thus likely it was to find the correct solution without getting any help. It enabled us to predict whether the naïve partners were likely to successfully operate the apparatus during testing by themselves and independent of the actions displayed by the trained individual. Each session lasted 15 minutes, until the eggs of all 40 trials were retrieved or lost, or when the individual did not touch the apparatus for five minutes. In case the individual continued to operate the apparatus on each session after session five but did not reach the criterion of retrieving the egg(s) on 32 out of 40 trials (80%), we continued to give more sessions up to a maximum of 15 sessions. If until then the individual was not able to find the solution herself and reach the criterion of retrieving egg(s) on 32 out of 40 trials, the ape transferred to the second step of training.

As a second step, behavioural *shaping* was done during which the experimenter trained the ape by shaping her responses on the apparatus. To decrease the difficulty of the task, we removed the springs and elastic band. The ape could now easily pull the handle towards her. Additionally, the handle was not pushed or turned back by either the springs or elastic band and stayed in the manipulated position. At the start of each session, the experimenter placed a lid on top of the apparatus, inserted a screw through an elongated slit in the lid, and fixated the screw in a small hole of the rod (see Figure 3.1C). The screw paralleled the rod with the lid, thereby making it impossible for the ape to turn the handle. This way, the experimenter forced the ape to perform other actions than immediately turning the handle and letting the egg fall into the black box. When the ape pulled the handle far enough that the next turning movement would cause the egg to fall onto the slide, the experimenter released the screw immediately. Since the handle was not pushed back by the springs and elastic band, it stayed in the manipulated position and the ape could turn the handle without any effort. In case the egg was successfully retrieved, the experimenter manually readjusted the rod to its original position. Another egg dropped into the cavity automatically and the experimenter again inserted the screw into the rod, starting a new trial. A maximum of 40 trials or 15 minutes were given per session (testing day). Depending on how successful the individual was, the experimenter switched from using the screw and blocking the turning to leaving the turning unblocked. This was done in a standardized manner corresponding to the level of skill of the individual (see Figure 3.4). The first 16 trials of the 40 total trials were always completed with the handle blocked. The ape passed into the third stage of training, if on the 2nd or any following session she successfully retrieved the egg(s) on 14 out of 24 (60%) trials without blocking.

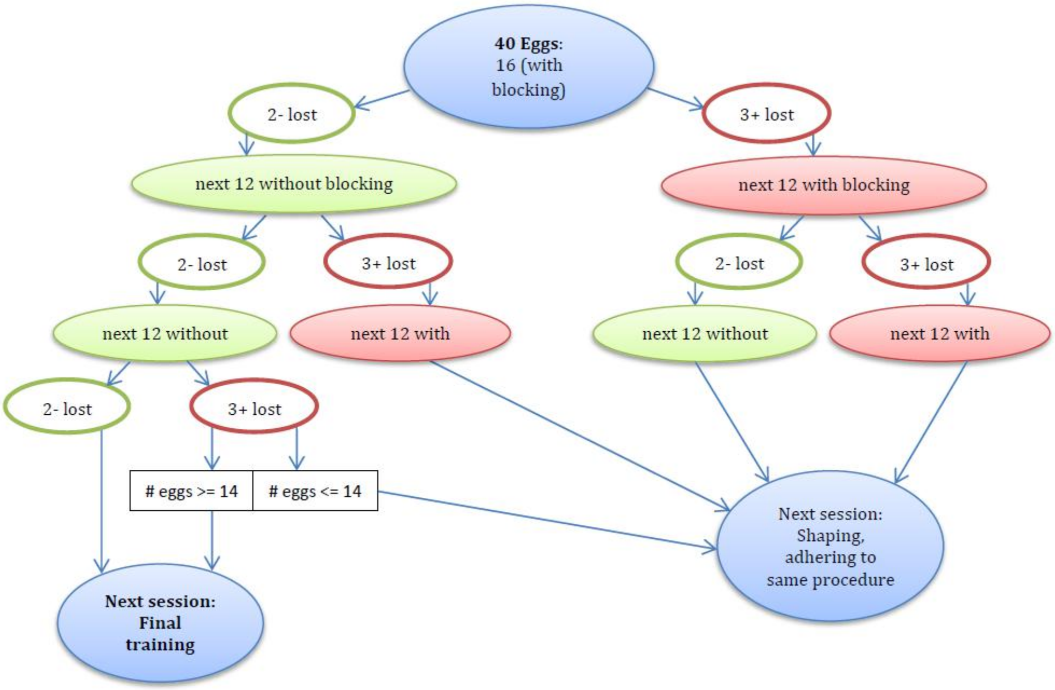


Figure 3.4 Standardized procedure of the training 'Shaping'. During this training the experimenter unblocked or blocked the handle so that the chimpanzee was not able to turn it depending on the number of eggs lost. We always blocked the first 16 trials, while the following 24 depended on the ape's performance.

As a *final* training, the experimenter first reinstalled the elastic band but not the springs. That way, the apparatus was automatically rebaited but the ape did not have to use a lot of strength to operate it. This was done in a standardized manner corresponding to the level of skill of the individual (see Figure 3.5). If the ape managed to successfully retrieve the egg(s) on 13 or more trials out of 40 (33%), the springs were added on the following session, thereby restoring the apparatus to its original configuration. In case the ape retrieved the egg(s) on 12 or less trials, the experimenter continued to present the apparatus only containing the elastic band until she reached the criterion. If the intact apparatus was presented and the ape retrieved the egg(s) on 12 or less trials, the experimenter again removed the springs on the next session. This procedure was continued until the ape successfully retrieved the egg(s) on 32 out of 40 trials (80%) with the springs inside, hence, with a fully intact apparatus. In that case, the ape passed into the test (hereafter, called 'subject').

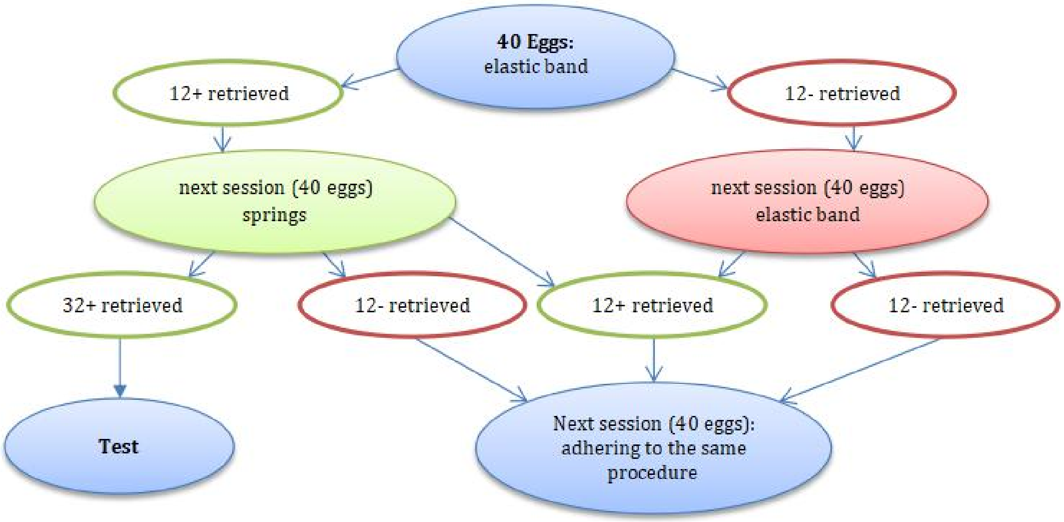


Figure 3.5 Standardized procedure of the final training. During this training the experimenter switched between installing the elastic band into the apparatus or additionally the springs, depending on the number of eggs retrieved.

Table 3.2 shows the number of sessions that each subject needed to pass into the test. None of the subjects, except Daza (who was the only chimpanzee that was a naïve partner before starting training), passed into the test without receiving behavioural shaping. This shows that the task was sufficiently difficult and the chances that naïve partners would perform the correct motions through asocial learning were minimal.

Table 3.2 The number of sessions that each individual needed to pass into the next training phase and test. Numbers in brackets indicate the total amount of sessions that either the elastic band ('eb') or the springs ('s') were installed during the final training. Daza was a naïve subject first before we trained her to become an expert, and had already somewhat learned how to retrieve eggs.

Subject	**Experiment**	**Solitary**	**Shaping**	**Final**
Jahaga	Independent	15	2	10 (3eb, 7s)
Alex	Independent	6	4	13 (5eb, 8s)
Kofi	Independent	5	3	9 (3eb, 6s)
Tai	Dependent	15	2	5 (1eb, 4s)
Lome	Dependent	8	3	6 (2eb, 4s)
Daza	Dependent	7	-	-

3.2. Training between experiments

Half the subjects started with experiment 'Independent' and subsequently switched to experiment 'Dependent'; the remaining half received the opposite order. Depending on which experiment was presented first, we trained the subject to either use 'apparatus single' (when starting with experiment 'Independent') or 'apparatus double' (when starting with experiment 'Dependent'). After completing the respective experiment and before switching to the other, the subject received another training phase to familiarize her with the new apparatus even though the mechanism was the same. This ensured that the expert understood the contingencies of the next experiment.

The procedure was the same as the solitary exploration phase of the initial training. Therefore, an intact apparatus was presented to the individual and no help was provided. Given that the individuals already knew the general mechanism we only gave 20 instead of the initial 40 trials. This also resembled the amount of sessions they received during test sessions and ensured that individuals remained familiar with the contingencies of the test. Again, each ape received a minimum of five sessions and each session either lasted 15 minutes, until all eggs were retrieved or lost, or when the ape did not touch the apparatus for five minutes. The criterion for passing into the test was again successfully retrieving 80% of the eggs, which in this case were 16 out of 20 trials.

3.3. Test – Experiment "Independent"

Each subject was paired with two different chimpanzees that fulfilled different roles. The constellation of pairs remained the same throughout the study (for two exceptions see Table 3.1, Jahaga and Kofi). Depending on the condition, one or none of the partners sat in an adjacent cage. 'Apparatus single' was mounted to both cages and a magazine containing ten eggs was attached to both apparatuses (see Figure 3.6A). We included three conditions.

In the test *condition 'Naïve',* the partner was a chimpanzee that was unfamiliar with the apparatus. This naïve partner had to operate the apparatus herself without any guidance from the experimenter. This test condition functioned to assess if the trained chimpanzees would change their own behaviour to demonstrate the correct actions. Given that the apparatus presented to the subject was also baited, she could operate her own apparatus independent of the partner's skill. To control for the influence of another individual merely being present instead of being naïve, we included the control *condition 'Expert'*, in which another previously trained individual was the partner and could operate the apparatus. Additionally, to acquire a baseline measure of how demonstrators acted when no individual was present, we included the control *condition 'Empty'*, in which no partner was present but the other apparatus was still baited. Each subject received one session of all three conditions on each testing day in a counterbalanced order across testing days. In each session it was possible for both apes to complete a maximum of 20 trials (two full magazines). A session lasted three minutes or until the eggs of the partner were either retrieved or lost. The subjects received a total of six testing days.

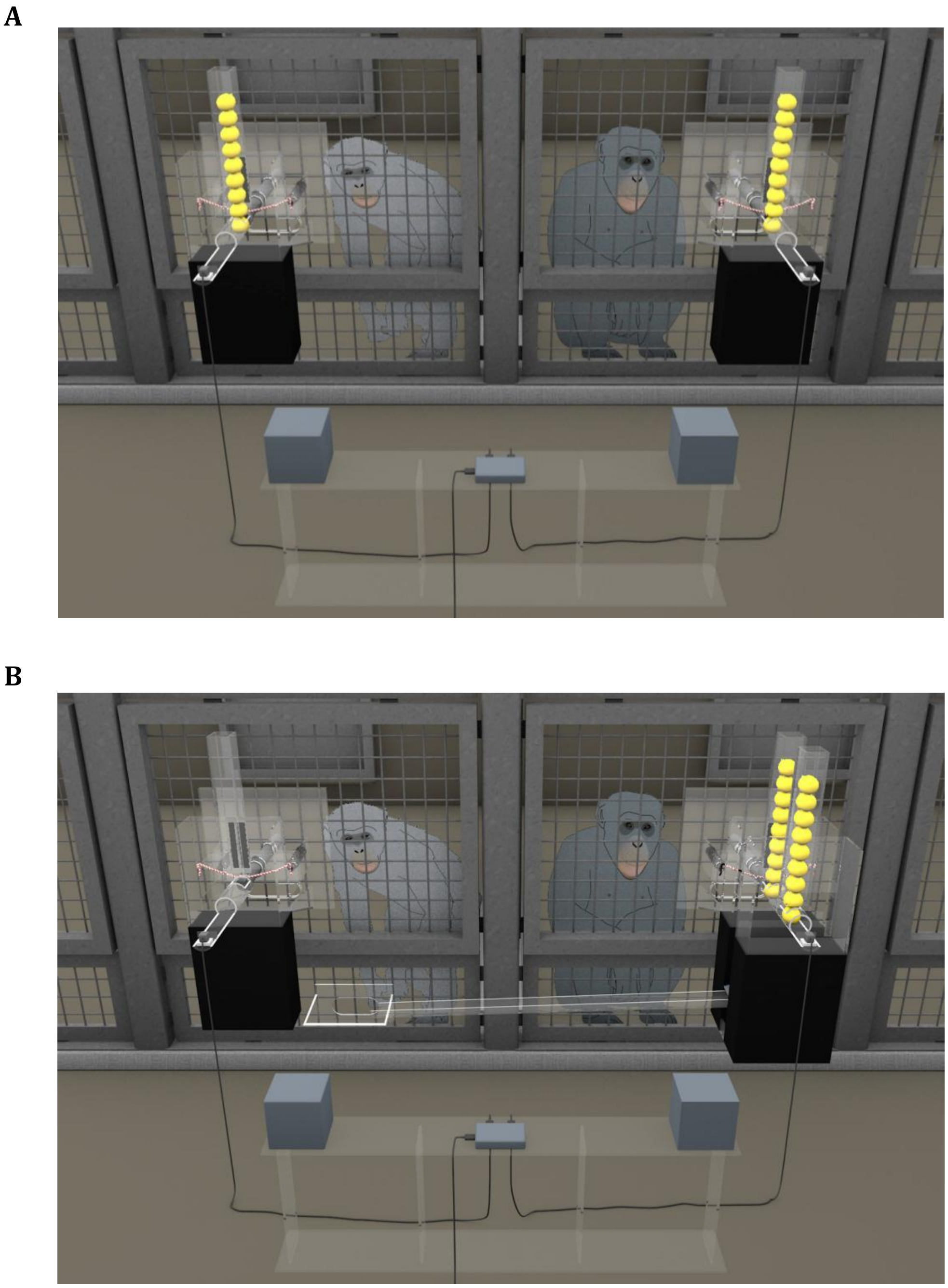


Figure 3.6 Set-up of experiment 'Independent' (A) and experiment 'Dependent' (B).

3.4. Test – Experiment "Dependent"

The composition of pairs (for one exception see Table 3.1, Daza) and the general set-up was the same as in experiment 'Independent'. Subjects received six sessions with each 20 trials per condition. One session of each condition was given per testing day and each session lasted three minutes or until all eggs of the partner were either retrieved or lost. The crucial difference to experiment 'Independent' was that we presented the subjects' partner with 'apparatus double' instead of 'apparatus single' (see Figure 3.6B). The subject herself still received 'apparatus single' but it remained empty throughout the entire experiment. Therefore, the subject was not able to retrieve any rewards herself. Instead, rewards could only be gained in case the partner successfully operated 'apparatus double'. As was described earlier, 'apparatus double' simultaneously provided a reward to the operating individual and to the adjacent cage, in which now the subject was located. The subject was therefore dependent on the conspecific and her ability to operate the apparatus and would gain a direct benefit from the subject acquiring the necessary skills.

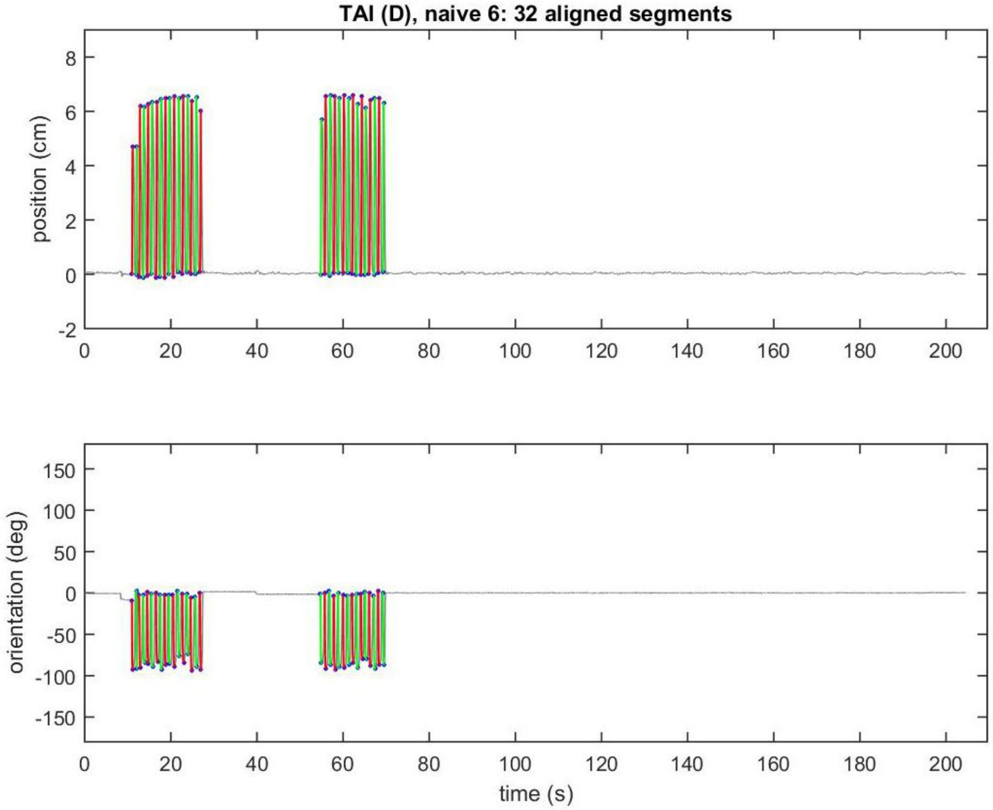
We included the same three conditions as in experiment 'Independent' for the same reasons as stated above. Additionally, we included a fourth condition, called *'Social Facilitation'*, which acted as a third control to our test condition. As was stated earlier, the mere presence of a conspecific might have influenced the subject's behaviour unrelated to the fact that she was naïve. Due to the change in set-up, condition 'Expert' was not sufficient anymore to rule out such a possibility because the subject's partner was successfully operating the apparatus and providing rewards to the subject. Thus, the likelihood that teaching might occur was directly reduced because the subject was occupied with collecting the eggs. This was not an issue in experiment 'Independent' since the subject was occupied with operating her own apparatus in any of the conditions. In the new set-up, condition 'Expert' now controlled for the fact that another but not naïve individual was present and able to access 'apparatus double' but left open the question of how the subject would behave when another individual is present but not able to access an apparatus. Condition 'Social Facilitation' therefore answered the question whether teaching was done merely because a partner was present without the need to acquire knowledge. Originally, we planned to use the naïve partner in this control condition; however, due to experimental error half the subjects were paired with the expert partner (see Table 3.1). Thus, for one half of the subjects we used the naïve partner as the social facilitation partner and for the other half we used the expert partner. Nevertheless, given that the partner was not able to access the apparatus, we think her level of expertise should not alter the purpose of this control condition.

We counterbalanced the order of conditions presented each day across and not within subjects as we included four conditions but only six testing days. Therefore, we formed each possible combination and pseudo-randomly distributed them across subjects, so that in the end each combination was given to two different pairs.

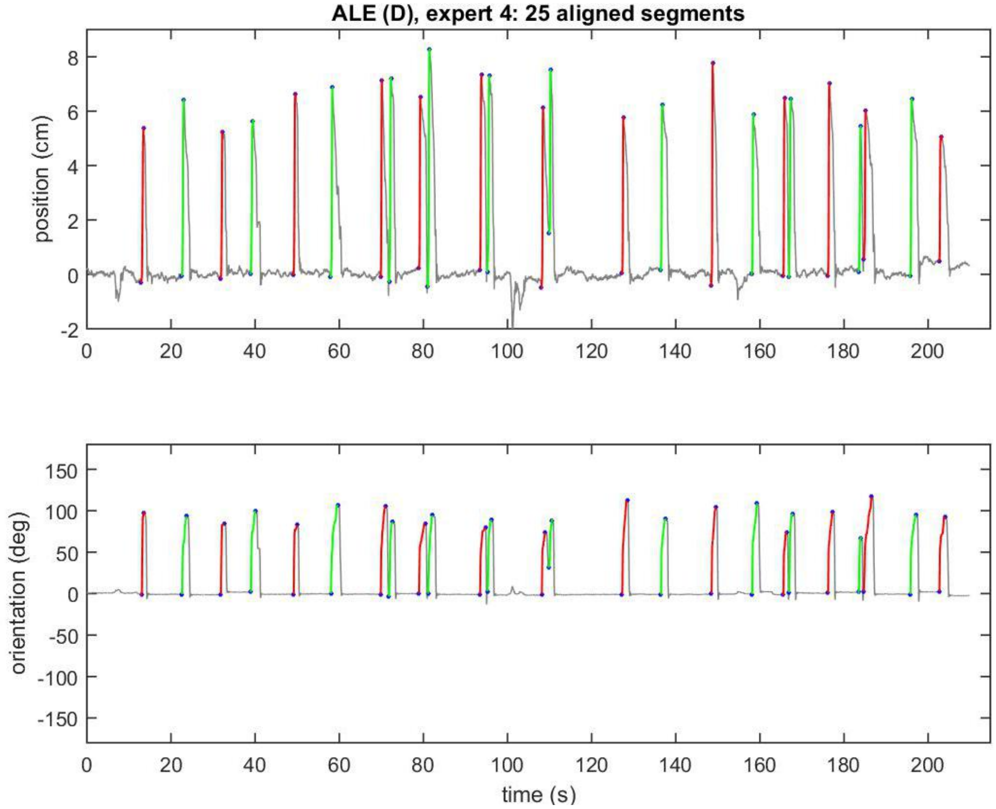
4. Data Coding

We used a Polhemus G4 motion tracking system, which captured the exact movements that each individual performed on their respective apparatus with a constant sampling rate of 120 Hz. The data was recorded by Matlab (2015) that we ran on an Asus computer with Microsoft Windows 8.1 as the operating system. We used two Polhemus hubs that each created a magnetic field, in which the exact position of the sensors could be tracked. To both apparatuses we attached one sensor to the rear end of the rod that connected to the handle (see Figure 3.1A&B). The sensors were linked to the Polhemus tracking system, which captured the data and sent it to the computer. Therefore, any changes in the sensors' position were recorded in real-time and stored for analysis. We recorded all horizontal movements (i.e. pulling) and any rotation (i.e. turning) performed with the handle over the course of the entire three minutes of each session (see Figure 3.7). The technology allowed us to detect subtle changes in the motions performed on the respective apparatus.

A


TAI (D), naive 6: 32 aligned segments
position (cm)
8
6
4
2
0
-2
0
20
40
60
80
100
120
140
160
180
200
orientation (deg)
150
100
50
0
-50
-100
-150
time (s)

B


ALE (D), expert 4: 25 aligned segments
position (cm)
8
6
4
2
0
-2
0
20
40
60
80
100
120
140
160
180
200
orientation (deg)
150
100
50
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-50
-100
-150
time (s)

C

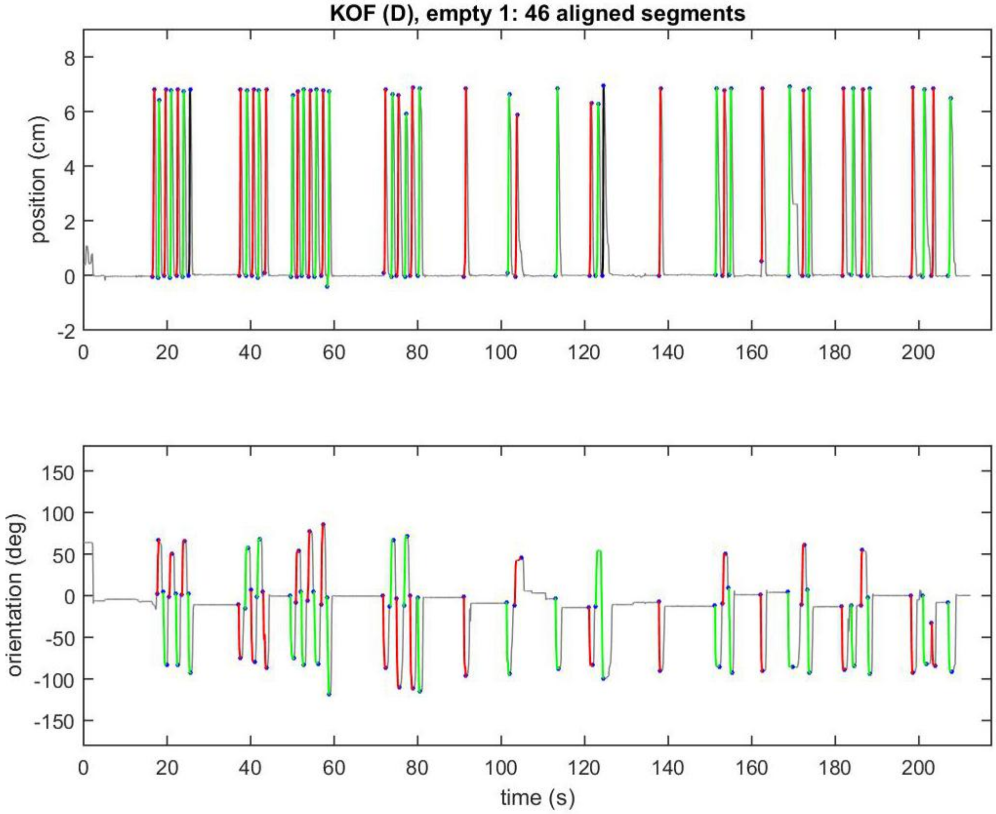


Figure 3.7 Example session of condition 'Naïve' (A), 'Expert' (B), and 'Empty' (C) in experiment 'Independent' when the demonstrators could gather eggs with their own apparatus. The three plots are selected not to represent the respective condition but to show different styles of manipulating the apparatus. The top graph of each plot shows the pulling movements and the lower graph the turning movements. Rotating the handle clockwise is represented by values that have a negative sign and rotating the handle counter-clockwise is represented by positive values. Complete movements (i.e. co-occurring pulls and turns) are coloured either in red or green and the two colours alternate to enhance visibility. Incomplete movements are coloured in black. Blue dots represent the start and peak of each movement.

In addition, we video recorded each session with three different cameras: Two recorded the cage of the subject and partner, respectively, and the third recorded the two apparatuses. We coded whether solicitation behaviours were exhibited by any of the conspecifics to attract the attention of their partner. We recorded the occurrence of banging against the mesh or glass separating the two individuals, which we operationalized as using hand or feet to hit against the surface thereby producing a loud sound. We also coded the occurrence of reaching through the mesh or small window made out of mesh below the glass, which we operationalised as extending at least one finger through the mesh separating the two cages. We used Solomon Coder to code the described behaviours. All videos were coded by the first author and 67% of these videos were coded by Anja Hutschenreiter. Both coders agreed that no solicitation gestures occurred for any of the apes.

5. Data Analysis - General Information

I will first describe the general statistical tools that we used before going into detail about the specific analyses that we performed to answer the different questions. I will discuss these analyses and the corresponding results as separate sections for the two experiments. Thus, the first section encompasses the analyses and results for the data of experiment 'Independent', and the subsequent section encompasses the analyses and results of experiment 'Dependent'. Finally, the chapter closes with a section in which I will discuss all results.

To understand whether subjects adapted their behaviour in the presence of a naïve partner while solving the task, we analysed the behaviour and kinematics of the demonstrator (i.e. our subject). None of the chimpanzees, demonstrators and partners, exhibited banging or reaching to attract the attention of their respective partner. Thus, we only assessed whether the demonstrators used their own apparatus to teach and what factors influenced the data collected by the Polhemus motion tracker.

All models were fitted in R (version 3.4.4; R Core Team, 2018). For the linear mixed models (LMM; Baayen, 2008) we used the function lmer, for the Generalized Linear Mixed Model (GLMM; Baayen, 2008) we used the function glmer, and for the negative binomial GLMM we used the function glmer.nb; each provided by the package 'lme4' (Bates et al., 2015) and with the level of significance set to 0.05. For the zero-inflated negative binomial Generalized Linear Model (GLM; Baayen, 2008) we used the function zeroinfl provided by the package 'pscl' (Zeileis, Kleiber, & Jackman, 2008).

To check the overall significance of the respective key predictors of the final model, we ran a maximum likelihood ratio test that compared the full model with a null model from which the key predictors were omitted (Forstmeier & Schielzeth, 2011). Only if the comparison between the full and null model reached significance did we investigate the effect of the individual key predictors. Moreover, we excluded nonsignificant interactions only when the full-null comparison was significant in order to be able to assess the influence of the main effects.

We evaluated whether the assumptions of the models were fulfilled. For the LMMS, we visually inspected qqplots and plots of the residuals plotted against the fitted values to gauge whether the assumption of normality and homoscedasticity of the residuals were met. No obvious deviations could be detected. To rule out collinearity, we inspected Generalized Variance Inflation Factors (GVIF; Fox & Weisberg, 2011) of all models, and excluded their respective random effects and interactions to do so. The function vif provided by the R package 'car' was used (Fox & Weisberg, 2011) and revealed no collinearity problem with any of our models (maximum VIF = 1.001; Zuur et al., 2010). Finally, we investigated whether the model parameters obtained from the full models were stable by excluding the respective random effects one at a time from the data (the R-function was written by Roger Mundry and is available upon request). Comparing the model parameters with those obtained by excluding levels of the random effects one at a time showed that the model parameters were fairly stable and no influential cases existed in each of the models.

As was explained above, I will now discuss the analyses and results of experiment 'Independent' before continuing to discuss the analyses and results of experiment 'Dependent'.

C. Experiment 'Independent' – Analyses and Results

1. Analyses

Due to too much noise in the data, we could not make use of some sessions during test days one to four of subject Daza. We therefore excluded all sessions of the three conditions for these test days because we would not have the full set of test and control measures. Thus, for subject Daza we only used session five and six for each condition. We performed two analyses and assessed whether demonstrators slowed down and separated the two actions differently depending on the condition.

1.1. Duration until peak

We reasoned that teaching would include slowing down, so that each movement is visually more accessible for the observer. Therefore, we assessed whether the duration to reach the peak of each movement was influenced by the condition in which apes were tested in. To understand whether this was the case, we fitted a LMM with a Gaussian error structure and an identity link function (McCullagh & Nelder, 1989). The number of observations was 6155 of 6 dyads. Our response variable was the duration to reach the peak of each movement. It was heavily right skewed and we needed to transform it by subtracting the minimum value from each original value and taking the square root of these. The variable condition (Naïve, Expert, Empty) and its interaction with the type of movement (Pull, Turn) was included to assess whether chimpanzees might have executed one but not both movement types slower in a given condition.

To control for the main effect of the type of movement we included this variable as a fixed effect in the null model. Moreover, to control for the effect that time might have had on the behaviour of the demonstrators, we included the session number (1-6) and z-transformed it before including it in the model. As a further variable, we included the sex of the demonstrator (F, M). We incorporated the random intercept (Barr et al., 2013; Forstmeier & Schielzeth, 2011) for subject identity, and the random slopes components (Barr et al., 2013; Forstmeier & Schielzeth, 2011) within subject identity for the type of condition, type of movement, and session. Additionally, we incorporated the random intercept (Barr et al., 2013; Forstmeier & Schielzeth, 2011) for test day identity, which is composed of the subject identity and session number, and the random slopes components (Barr et al., 2013; Forstmeier & Schielzeth, 2011) within test day identity for the type of condition and type of movement.

1.2. Separation of movements

We further reasoned that teaching would possibly include separating the two movements to make them easier to follow for the observer, which would result in a greater duration between the onset of the pulling movement and the onset of the turning movement. The most efficient strategy is to start turning shortly after pulling, so that both the minimal distance and minimal degree required to retrieve an egg are co-occurring. In case chimpanzees use their own apparatus to demonstrate the two movements, one way to make the movements more visible is to separate the two. This would result in a greater duration between the points in time that chimpanzees started to turn once they pulled. We fitted another LMM with a Gaussian error structure and an identity link function (McCullagh & Nelder, 1989). The number of observations was 2934 of 6 dyads. Our response variable was the duration between the start of the pulling movement to the start of the turning movement of all complete movements (i.e. pulls and turns that overlapped). For a movement to be considered complete the onset of a pull movement had to occur before the peak of a turn movement, or the turn onset had to occur before the pull end. Thus, in most cases a retrieved egg resulted from complete actions. We added condition with three levels (Naïve, Expert, Empty) as our sole predictor.

Again, as in the previous model, we included the demonstrator's sex (F, M) and the z-transformed variable session number (1-6) as control factors. We again included the random intercept (Barr et al., 2013; Forstmeier & Schielzeth, 2011) for subject identity and test day identity, and the random slopes component (Barr et al., 2013; Forstmeier & Schielzeth, 2011) within subject identity for the type of condition and session and within test day identity for the type of condition.

2. Results

Across conditions, chimpanzees operated their baited apparatus on 107 of 108 sessions at least once. Only one subject did not operate the apparatus during one session of condition 'Empty'. To understand whether demonstrators adapted their behaviour in the presence of a naïve individual that could operate her own apparatus, we assessed 1) whether demonstrators slowed down and 2) whether they separated their movements.

2.1. Duration until peak

We assessed whether chimpanzees slowed down while manipulating their own apparatus as a function of condition. Slowing down would be beneficial to the partner, as it makes the movement visually more accessible. The LMM that included the predictor condition and its interaction with the type of movement explained a significant amount of the variance of why chimpanzees slowed down (χ^2 = 14.55, *df* = 4, *N* = 6155, *p* = .006, Table 3.3). The significant interaction between condition and type of movement (χ^2 = 8.34, *df* = 2, *p* = .015) reveals that chimpanzees slowed down in some conditions and the pattern was different for the two movements. Figure 3.8 shows that turn movements were exhibited similarly fast in the two social conditions (i.e. 'Naïve' and 'Expert'), while chimpanzees slowed down when there was no partner present (i.e. 'Empty'). With regard to pull movements, chimpanzees exhibited these actions differently fast in each condition. They pulled fastest when another trained individual simultaneously manipulated an apparatus (i.e. 'Expert') and again slowest when no partner was present. Thus, both turn and pull movements were exhibited slowest in the condition 'Empty', while pull but not turn movements were exhibited fastest in the condition 'Expert'.

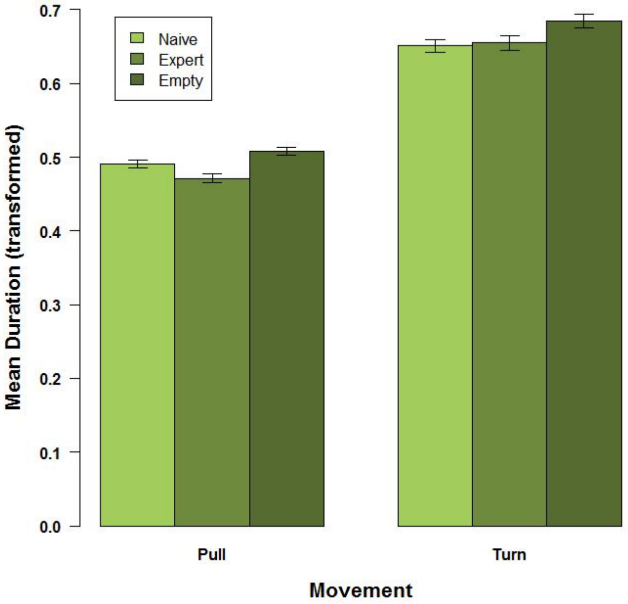


Figure 3.8 Depiction of the differences between pull and turn mean durations in each of the three conditions while controlling for the effect of session and sex of the demonstrator. 95% confidence intervals are displayed.

Table 3.3 Results of the LMM that assessed whether the variable condition and its interactions with the type of movement influenced the duration until chimpanzees reached the peak of pulling and turning movements.

Term	Estimate	SE	lower CI	upper CI	*Z*	*P*
Intercept	0.47	0.12	0.18	0.77	(3)	(3)
Condition						
Naïve vs Expert	-0.00	0.01	-0.03	0.03	(3)	(3)
Naïve vs Empty	0.02	0.01	-0.01	0.05	(3)	(3)
Sex Dem F vs M	0.05	0.16	-0.33	0.42	0.09(2)	.763(2)
Mov. Type Pull vs Turn	0.16	0.04	0.07	0.26	(3)	(3)
Session(1)	-0.00	0.01	-0.03	0.03	0.09(2)	.769(2)
Condition*Mov. Type					8.34(2)	.015(2)
Naïve vs Expert	0.03	0.01	0.01	0.05	(3)	(3)
Naïve vs Empty	0.02	0.01	-0.00	0.04	(3)	(3)

(1) standardized to its mean
(2) overall effect of the predictor
(3) not shown because of limited interpretation

2.2. Separation of movements

We further assessed whether the duration between the onset of the pulling and onset of the turning movement was different between conditions, but found the LMM to be non-significant (χ^2 = 3.09, *df* = 2, *N* = 2934, *p* = .213; Table 3.4). Therefore, chimpanzees did not separate the two movements more in any of the conditions.

Table 3.4 Results of the LMM that assessed whether the variable condition influenced the duration between the start of the pulling and the start of the turning movement.

Term	Estimate	SE	lower CI	upper CI	*Z*	*P*
Intercept	-0.01	0.04	-0.11	0.08	(3)	(3)
Condition					3.09(2)	.213(2)
Naïve vs Expert	-0.03	0.02	-0.08	0.02	(3)	(3)
Naïve vs Empty	-0.03	0.02	-0.08	0.02	(3)	(3)
Sex Dem F vs M	-0.05	0.05	-0.17	0.06	1.1(2)	.295(2)
Session(1)	-0.00	0.01	-0.02	0.02	0.14(2)	.71(2)

(1) standardized to its mean
(2) overall effect of the predictor
(3) not shown because of limited interpretation

D. Experiment 'Dependent' – Analyses and Results

1. Analyses

We again assessed whether chimpanzees used their own apparatus to teach and what factors influenced their kinematics. Given that in experiment 'Dependent' the demonstrator faced an empty apparatus, the manipulation rates were much lower than in experiment 'Independent', which resulted in not sufficient data to perform the same analyses as in experiment 'Independent'. We therefore only assessed whether chimpanzees operated their empty apparatus to a different frequency depending on the condition. This measure was obsolete in experiment 'Independent' as the demonstrator manipulated the own apparatus to retrieve eggs herself in every condition.

1.1. Frequency of total manipulations

To understand whether demonstrators would operate their empty apparatus more frequently when a naïve individual was present that actually needed help to solve the task, we fitted a GLMM with a Poisson error structure and log link function (McCullagh & Nelder, 1989). The model was over-dispersed with a dispersion parameter of 1.63 ($\chi^2 = 445.56$, $df = 273$, $p < .001$). We therefore fitted a GLMM with a negative binomial Poisson model and log link function, which also did not converge due to an inflated number of zeros in the data. Thus, we used a zero-inflated negative binomial GLM, which was not over-dispersed and converged. The number of observations was 288 of 6 subjects. Our response consisted of the separate count of pull and turn movements executed by the demonstrator. The model comprised the variable condition (Naïve, Expert, Empty, SF) in the zero part of the model since we assumed that it is the condition that led to low rates of manipulations. In the count part of the model, we included condition and its interaction with session number (1-6) to assess whether chimpanzees manipulated their apparatus more often in one of the conditions and whether this might have been influenced by the time that passed. Session was z-transformed before inclusion.

We included the main effect of session, the sex of the demonstrator (F, M), and the type of movement (Pull, Turn) to control for their influence.

1.2. Frequency of complete manipulations

In the previous model, we included all movements that the demonstrator performed on the empty apparatus. Therefore, we also considered incomplete movements that consisted only of one of the two actions. To understand whether more complete movements (i.e. pulls and turns that overlapped) occurred in the test compared to the control conditions we fitted an additional model. This enabled us to gauge whether chimpanzees might perform the entire action sequence more often when the naïve partner needed to learn which actions have to be executed in which order. As was stated previously (section C1, 1.2.; p. 109) for a movement to be considered complete the onset of a pull movement had to occur before the peak of a turn movement, or the turn onset had to occur before the pull end. Thus, we only included movements that were executed in the correct order to potentially acquire an egg. We fitted another GLMM with a Poisson error structure and log link function (McCullagh & Nelder, 1989). Due to the fact that the GLMM was over-dispersed with a dispersion parameter of 1.49 ($\chi^2 = 194.57$, $df = 131$, $p < .001$), we fitted a negative binomial Poisson model with a log link function. The number of observations was 144 of 6 subjects. Our response was the count of complete movements. As our key predictors, we included condition and its interaction with the z-transformed session number (1-6) to assess the effect that time might have had on the differences between conditions.

As in the previous model, we included the main effect of session and the sex of the demonstrator (F, M) to control for their influence. Furthermore, we incorporated the random intercept (Barr et al., 2013; Forstmeier & Schielzeth, 2011) for subject identity, and the random slopes component (Barr et al., 2013; Forstmeier & Schielzeth, 2011) within subject identity for the type of condition and session.

2. Results

Across conditions, chimpanzees operated their empty apparatus on 39 of 144 sessions at least once. To understand whether demonstrators adapted their behaviour in the presence of a naïve individual that could operate an own apparatus, we assessed 1) whether demonstrators generally operated their apparatus more frequently in the test condition compared to the control conditions and 2) whether the frequency of complete movements was greater in the test than the control conditions.

2.1. Frequency of total manipulations

The zero-inflated GLM that included the variable condition and its interaction with session number in the count part and the variable condition in the zero part explained significantly more variation of why manipulations occurred than a model from which the variable condition and its interaction were excluded from the count part ($\chi^2 = 13.86$, $df = 6$, $N = 288$, $p = .031$).

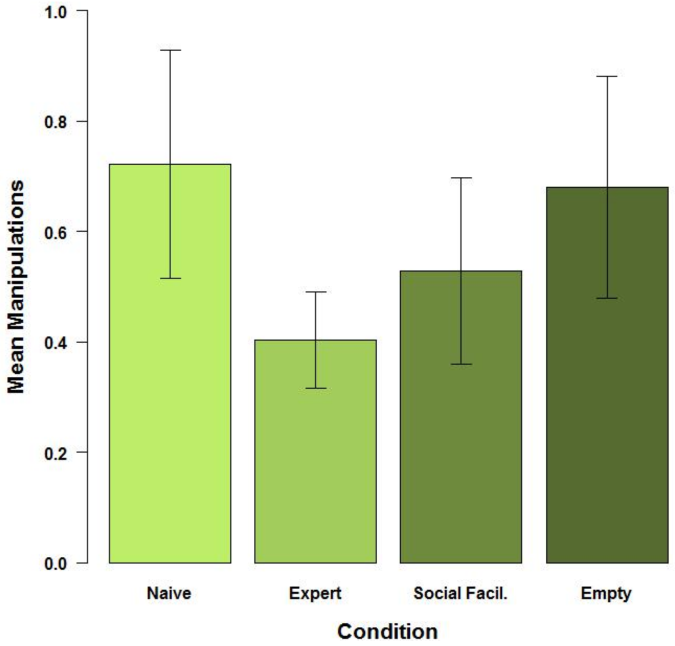


Figure 3.9 Mean values of manipulation rates in a given session for each condition of experiment 'Dependent' while the effect of the demonstrator's sex, session number, and type of movement are controlled for. 95% confidence intervals are displayed.

Given that the interaction between condition and session number was not significant, we omitted it to be able to assess the main effect of condition. The new model also yielded a significant result ($\chi^2 = 11.27$, $df = 3$, $N = 288$, $p = .010$; Table 3.5) and revealed that condition influenced the manipulation rates performed on the empty apparatus ($\chi^2 = 15.84$, $df = 3$, $p = .001$). Chimpanzees operated their apparatus significantly less often when another trained individual was present (i.e. 'Expert') than a naïve individual that had access to an apparatus (i.e. 'Naïve'), while there was no difference between each of the other conditions (Figure 3.9).

Table 3.5 Results of the zero-inflated GLM indicating whether the variable condition explained the amount of total manipulations exhibited.

Term	Estimate	SE	lower CI	upper CI	χ^2	*P*
Count Part						
Intercept	1.1	0.47	0.18	2.01	(3)	(3)
Condition					15.85(2)	.001(2)
Naïve vs Expert	-1.81	0.46	-2.71	-0.91	(3)	(3)
Naïve vs SF	-0.88	0.54	-1.94	0.19	(3)	(3)
Naïve vs Empty	-0.84	0.57	-1.94	0.27	(3)	(3)
Sex Dem F vs M	-0.88	0.34	-1.54	-0.22	6.84(2)	.009(2)
Session(1)	-0.22	0.13	-0.47	0.03	3.09(2)	.079(2)
Mov. Type Pull vs Turn	0.24	0.28	-0.30	0.79	0.77(2)	.380(2)
Zero Part						
Intercept	0.58	0.48	-0.35	1.51	(3)	(3)
Condition						
Naïve vs Expert	-8.80	67.82	-141.72	124.11	-0.13	.897
Naïve vs SF	-0.59	0.71	-1.99	0.81	-0.83	.407
Naïve vs Empty	-0.64	0.75	-2.12	0.84	-0.85	.396

(1) standardized to its mean
(2) overall effect of the predictor
(3) not shown because of limited interpretation

2.2. Frequency of complete manipulations

Finally, we investigated whether more complete movements occurred in the test than the control conditions, which would show that demonstrators used coherent movements in the presence of a naïve individual that could deliver eggs to the demonstrator. The full model did not explain significantly more of the variance of whether complete movements occurred than the respective null model ($\chi^2 = 2.65$, *df* = 6, *N* = 144, *p* = .852; see Table 3.6), so chimpanzees exhibited complete movements to a similar degree in all four conditions and not in response to a naïve individual being present that could have distributed eggs to them.

Table 3.6 Results of the GLMM that assessed whether the variable condition and its interaction with the session number influenced the amount of complete movements exhibited. Bootstrapped 95% CIs used.

Term	Estimate	SE	lower CI	upper CI	χ^2	*P*
Intercept	-0.51	0.53	-2.11	0.20	(3)	(3)
Condition						
Naïve vs Expert	-0.76	0.85	-4.59	1.22	(3)	(3)
Naïve vs SF	-0.51	0.67	-2.39	1.02	(3)	(3)
Naïve vs Empty	-0.32	0.64	-2.51	1.24	(3)	(3)
Sex Dem F vs M	-0.9	0.48	-2.02	-0.00	3.17(2)	.075(2)
Session(1)	-0.57	0.47	-1.75	0.46	(3)	(3)
Condition*Session(1)					1.84(2)	.607(2)
Naïve vs Expert	-0.39	0.74	-3.14	1.22	(3)	(3)
Naïve vs SF	0.49	0.60	-1.13	2.11	(3)	(3)
Naïve vs Empty	0.05	0.59	-1.79	1.64	(3)	(3)

(1) standardized to its mean
(2) overall effect of the predictor
(3) not shown because of limited interpretation

E. Discussion

Across conditions of experiment 'Independent', chimpanzees operated their baited apparatus on 107 of 108 sessions at least once. In this experiment, chimpanzees performed both types of movements significantly slowest when no partner was present (i.e. condition 'Empty'). While there was no difference between the two social conditions (i.e. condition 'Naïve' and 'Expert') with regard to turning movements, chimpanzees exhibited pulling movements significantly fastest when another trained individual was present in comparison to a naïve partner. Our second analysis showed that chimpanzees did not separate the two movements more in any of the conditions. In experiment 'Dependent', chimpanzees operated their empty apparatus on 39 of 144 sessions at least once. While they generally manipulated their apparatus significantly less often when another trained individual was present (i.e. 'Expert') in comparison to a naïve individual that had access to an apparatus (i.e. 'Naïve'), there was no significant difference between the test and the other two control conditions. We did not find evidence that chimpanzees used complete movements (i.e. co-occurring pulls and turns) more often in the presence of a naïve individual that could deliver eggs to the demonstrator. They performed entire action sequences to a similar degree in all four conditions.

Our results do not provide evidence that chimpanzees actively modified their behaviour in the presence of a naïve individual, even when they themselves could have benefitted from transmitting relevant knowledge. Thus, neither did they slow down or separate their movements, nor did they exhibit a higher frequency of manipulations in general or a higher frequency of sequencing both movements in response to being paired with a naïve partner. In experiment 'Independent', we did find that chimpanzees seemed to operate their own apparatus slowest to retrieve eggs when they were by themselves without a conspecific present. Furthermore, they pulled faster when another trained individual simultaneously operated a second apparatus to retrieve eggs in the neighbouring cage than when an individual was present that only tried to retrieve eggs. One explanation of the differences between the three scenarios might be that chimpanzees perceived the game to be competitive and this influenced them to a greater degree when the conspecific actually gathered eggs as well. However, during training and test they could have realized that the two apparatuses were not connected and they could gather their own eggs independent of the conspecific. Another more likely explanation might be that response facilitation influenced the activity of our subjects. Response facilitation accounts for an increase in an activity upon being exposed to another individual that engages in the same behaviour (Hoppitt & Laland, 2008). Thus, the observed increase in speed might have been due to response facilitation that, accordingly, should act more strongly in the condition 'Expert' than 'Naïve' as the other individual performed the same task and simultaneous to the subject. In experiment 'Dependent', we found that chimpanzees manipulated their empty apparatus less often when another trained individual was present in comparison to a naïve individual that had access to an apparatus, while they manipulated their apparatus to a similar frequency in each of the other three conditions (i.e. 'Naïve', 'Social Facilitation', 'Empty'). One explanation for the overall low frequency of manipulations in condition 'Expert' might be that in this condition chimpanzees were occupied with collecting the eggs distributed to them by their trained partner.

The conclusion that chimpanzees did not teach in this study cannot be explained by a lack of motivation given that in experiment 'Dependent' demonstrators would have benefitted from transmitting knowledge. Moreover, given that each subject completed a prior training, during which they often alternated between retrieving eggs and consuming them at both locations, and given that each day they received one session of condition 'Expert', we think that they did understand that a correct manipulation of 'apparatus double' produced eggs for themselves as well. Therefore, a lack of teaching in experiment 'Dependent' rules out that chimpanzees were generally not motivated to do so. As was discussed earlier, chimpanzees can form a representation of ignorance in others (Crockford et al., 2012), understand when another individual holds a wrong belief about situations (Krupenye et al., 2016), and understand when another individual performs actions that are inadequate to achieve a goal (Call et al., 2005). Crockford and colleagues (2012) further showed that they are also willing to inform others of potential danger when facing snakes in the wild. Moreover, chimpanzees are able to use foresight and inhibit immediate desires (Bräuer & Call, 2015; Osvath & Osvath, 2008). As each of these abilities was proposed to be necessary in order to teach and we controlled for the fact that chimpanzees might not be motivated to do so, the remaining explanation might be that they lack a full-blown theory of mind that is needed to identify the zone of proximal development of another individual.

We did not observe behaviours such as reaching or banging that might have been used to solicit the attention of the naïve individual. This corroborates previous experimental research investigating solicitation gestures or physical guidance in a teaching (Povinelli & O'Neill, 2002) and non-teaching context (Hirata & Fuwa, 2007). We also did not find solicitation behaviours on part of the observing naïve individual to request help or action of the demonstrator, possibly further diminishing chances of the demonstrator understanding that an action is required and the partner in need of help.

Two limitations need to be discussed. First, due to logistical reasons the partners of our trained subjects were all adult conspecifics that were either unrelated or maternal or fraternal siblings. As was discussed earlier, the only observations of potential teaching were observed in tool use contexts and between mothers or adult siblings and young chimpanzees. Helping behaviour in general should be greatest between mothers and their offspring due to inclusive fitness benefits. Nevertheless, in case chimpanzee mothers are able to teach, this cognitive ability should also be present in males and other females. Given that we took care of the fact that they might lack the motivation to do so, it would be sensible to assume that these chimpanzees would also exhibit teaching if chimpanzee mothers do so.

Secondly, the task itself introduced a new behaviour that is ecologically not relevant to chimpanzees, which might have decreased an intuitive understanding that the action needs to be taught. Yet, the tested population of chimpanzees was used to solving arbitrary tasks on a daily basis and succeeded in a multitude of such tasks as well. We could further show that each individual was able to obtain eggs using the two learned motions as each reached the high-set criterion during training, and they continued to succeed during test. Thus, even if they did not understand the exact mechanism of how the apparatus' mechanics worked, they were well able to perform the necessary actions, which was sufficient knowledge to teach their ignorant partners how to retrieve eggs. Therefore, we do not think that using an arbitrary task limited the chances for this specific population to exhibit their cognitive abilities. Furthermore, the advantage of teaching in general is that it can be flexibly used to transmit knowledge about a new problem.

Future research could still try to address both limitations and might benefit from including female adults and their infants and using a design that resembles stick or stone tool use. One possibility, for example, might be to carry out a longitudinal study that combines our idea of measuring subtle changes in motions, but introduces a new tool to female adults that are pregnant or while carrying babies. Once their infants are roughly one year old and until they are five, these females and their infants could be observed in a controlled setting while the mothers interact with the new tool. This would allow to identify whether the mothers start to use the tool differently than they had when their children were younger. The assessment could incorporate body position to enhance visibility for the infants or enabling infants to take tools by continuing to hold them in their hands, as Moore (2013) and Matsuzawa (2001, 2011) respectively suggested. Even though we - and other researchers - did not find any solicitation behaviours, future studies should still record their occurrence to assess Moore's (2013) idea of minimal pedagogy. Finally, a measure of gaze-alternation between the ignorant partner and the task in question could be incorporated. This could be used to assess whether chimpanzees either understand something about the task even if they might not be able to change their own behaviour in a way that could be helpful to their partner, or check whether the partner is looking before changing their behaviour.

In addition to age, future studies could also assess whether and how relationship quality and sex might influence teaching. Our sample size would have been too small to draw accurate conclusions regarding their individual influence. Therefore, we did not include a formal measure of relationship quality, but tested individuals that were known to get along well. Furthermore, we tested three males and females to reduce bias in our results, however, did not include sex as a factor in our models. As with relationship quality, sex could be included as a factor in case the sample size is large enough to understand whether males or females might be more likely to teach. Given that wild male chimpanzees seem to cooperate most often with one another but wild female chimpanzees should be the primary teachers of young chimpanzees, a sex difference would be of great interest to understand the motivation behind teaching and factors that might support it.

Another avenue to understand whether chimpanzees have the cognitive capacity to teach might be to use human partners instead of conspecifics. Hirata and Fuwa (2008) reported that solicitation gestures were only used to recruit help of a human but not conspecific partner. Additionally, Grosse and colleagues (2015) reported accurate demonstrations of an action towards a human partner. Even though it seems counterintuitive that captive chimpanzees are able to teach an individual of a different species but have trouble if it is an individual of their own, long term experience with humans and continued reinforcement after directive communication might have facilitated a sensitivity to more fine-grained communication to acquire food from humans. This might either enhance understanding of the task itself or result in an expectation that directive communication is worthwhile.

To sum up, with the current data we can rule out that chimpanzees are not teaching conspecifics because they are generally not motivated to transmit knowledge to these. We do not know whether they might not be able to adjust their own movements because they do not understand how to change a lack of knowledge in their partner due to a lack a full-blown theory of mind, or whether they do not expect that their communication will be understood by their conspecific. Using motion trackers to measure subtle changes in chimpanzees' actions proved to be possible and we were generally able to find changes in our subjects' motions. Thus, the design could be further adapted to incorporate our discussed limitations.

IV. Chapter 4: Teaching in children

A. Introduction

Teaching is thought to play an integral part in sustaining human culture (Kruger & Tomasello, 1996). It enables individuals to build upon the skills and knowledge of others and thus helps to acquire complex cumulative culture including advanced technologies and tools (Kruger & Tomasello, 1996). Even though a few researchers state that teaching can only be found in Western cultures (Lancy, 2016), others argue that teaching is universal among humans (Kline, 2015; Strauss et al., 2002). Csibra and Gergely (2009) go a step further and suggest that it is an innate and not learned ability of humans to be receptive to teaching. They propose the term 'natural pedagogy' and argue that children are naturally able to perceive communicative instances, such as teaching meant for them. Thus, upon recognizing ostensive signals directed at them (e.g. eye contact, infant-directed speech, changes in body position), children change how they learn about the content transmitted by the partner. Actions or information following ostensive signals will be interpreted as relevant even if they are apparently unnecessary (Brugger, Lariviere, Mumme, & Bushnell, 2007; Southgate, Chevallier, & Csibra, 2009). Ostensive signals convey intentions behind the message and children act accordingly and expect relevance of even redundant information communicated in such a way (Csibra & Gergely, 2009). Through this, they assume generalizability of the information and pay more attention to it (Csibra & Gergely, 2009). Given that children are receptive to ostensive cues even before they are able to use the information and learn its content, Csibra and Gergely (2009) argue that the "sensitivity to at least some of the ostensive signals is most likely to be innate" (p. 149). Yet, this approach only focuses on the receiver side of teaching and does not discuss whether children teach themselves, which processes constitute teaching in humans, and how they develop through ontogeny.

While we do not know the underlying motivation of teaching, a multitude of studies that assessed children's tendency to cooperate in other settings have been produced. To date, we know that children, for example, readily try to help adults reach their goal (Warneken & Tomasello, 2007), provide information by pointing towards the sought-after object (Liszkowski, Carpenter, Striano, & Tomasello, 2006), and share resources upon perceiving discomfort in an adult partner (Svetlova, Nichols, & Brownell, 2010). Hepach, Kante, and Tomasello (2017) argued that from these studies it is difficult to infer the motivation underlying even seemingly altruistic acts. Adults are a source of comfort and help, so children might only provide help to partners from whom they can in turn expect benefits. Yet, the researchers found children to be equally altruistic when facing a peer, which suggests that helping is indeed motivated by other-regarding preferences and not by expectations due to a history of receiving help. This claim is further supported by the finding that children helped anonymously (Hepach, Haberl, Lambert, & Tomasello, 2017) and that it did not matter whether children themselves or another person performed the act needed to fulfil the goal (Hepach, Vaish, & Tomasello, 2012; Hepach, Vaish, Grossmann, & Tomasello, 2016). The authors of these studies concluded that the main motivation is to see the goal of the other person fulfilled instead of gain recognition for their help and hence attain direct or indirect positive benefits. We can therefore assume that children tend to be genuinely concerned about others' well-being when they engage in altruistic acts. Given that teaching can be considered as an altruistic act and emerges around the same age that children engage in more complex altruistic behaviours (Svetlova et al., 2010), it is probable that similar motivations underlie this type of helping. Nevertheless, research that directly investigates the underlying motivations and its effect on teaching strategies is currently lacking for young children.

Understanding how teaching develops through life enables us to understand what constitutes teaching and what cognitive prerequisites need to be in place to support it. To reconstruct a possible developmental trajectory of abilities related to teaching, I will now review studies that sought to reveal which teaching strategies subjects used depending on their age.

Probably the earliest indication that children are willing to alter the knowledge state of another individual comes from pointing studies. Liszkowski, Carpender, Striano, and Tomasello (2006) showed that already *1-year-old* infants were able to use pointing to help an adult find the object that the adult searched for. Such informing and, thus, altering the knowledge state might be the earliest evidence that children understand that another individual lacks certain information and that this can be altered by their own actions. Nevertheless, it is unclear to what degree they can form a representation of ignorance and the means to communicate are still very limited.

Knudsen and Liszkowski (2012) investigated whether *1.5- and 2-year-olds* were able to anticipate where an adult would search for an object based on her true or false belief. They found that 1.5-year-olds pointed toward the actual location of the hidden object once the person holding a false belief returned to the scene and was about to retrieve the object. More than half of the 2-year-olds also verbally informed the mistaken adult about the correct location of the object and used utterances such as “in there”. Infants of both age groups did not inform the adult if she knew the new location of the object or if she was misinformed but had a different goal (i.e. cleaning a container instead of searching for the object). Thus, they only informed when the information was relevant to the adult with regard to the “adult’s prior goal representation and her representation of reality”. The authors suggested that children of this age already anticipated their partner’s next action and errors, and that they intervened without solicitation. However, it is not clear whether the children pointed with the actual intention to correct errors, or whether they might have pointed to the object because they perceived the adult to be searching. The latter interpretation would be more parsimonious and corroborate the finding obtained by Liszkowski and colleagues (2006).

Ashley and Tomasello (1998) tested children between the age of *2 and 3.5 years* and assessed whether they would teach a peer how to retrieve a sticker from an apparatus. Two-year-olds did not learn the task themselves and could thus not be tested as teachers. Children of all tested age groups rarely responded to their partner, explained how the task works in general, and gave generic directives to demand action of their partner. Even though 2.5-year-olds started to make adjustments in how they communicated with their partner (i.e. drawing attention to themselves or the task), only from the age of 3 onwards did they become increasingly sensitive to the partner’s lack of knowledge. These 3-year-olds started to use specific directives (i.e. stating the specific actions needed to operate the apparatus), but the frequency was still quite low. Only by the age of 3.5 did they attempt to teach in a more adapted and direct manner even though it still occurred relatively rarely. In comparison to the younger children, 3.5-year-olds used specific directives significantly more often and were the only age group that sometimes demonstrated the actions to their partner. Thus, it appears that children start to engage in teaching around the age of three and although they lack experience in how to teach. Strauss, Ziv, and Stein (2002) referred to this as 'unschooled cognition' and concluded that "if *very young children engage in teaching* and they have not been taught to teach, we might have another case for the claim that teaching is a natural cognition" (p. 1477).

Strauss and colleagues (2002) investigated how teaching strategies changed between *3- and 5-year-old* children and gauged its relation to 1) theory of mind abilities and 2) the understanding of their own actions as teachers. The researchers incorporated two classic false belief tasks (i.e. a doll that is searching a relocated object), two false belief tasks in the context of teaching (i.e. a teacher that has a false belief about a pupil's state of knowledge), and two tasks that assessed the comprehension of knowledge gaps between different individuals (i.e. one pupil is knowledgeable and a second is not). Subsequently, the researchers measured the children's ability to teach themselves when playing a board game they previously learned with a naïve partner. After the children taught the game to the naïve child they were asked how they did so and how they knew that the partner had learned. Both age groups were able to recognize that the partner had learned the game after they taught them and were also able to understand knowledge gaps between individuals, e.g. that one person can have more knowledge about something than another person. Even though 3-year-olds performed significantly lower on both sets of false belief tasks (classic and new) than 5-year-olds, they already attempted to teach. Nevertheless, the strategies to teach differed between the two age groups with 3-year-olds mainly relying on demonstrations and 5-year-olds on verbal explanations. Furthermore, 5-year-olds started to be responsive to errors made by the partner and repeated explanations given before but in a shorter manner. They additionally used direct questions to assess whether the partner was able to play the game now. The difference in teaching strategies was also reflected in the way children talked about how they taught their partner. Three-year-olds described their own actions ("I moved the train and stopped it at a station."), while 5-year-olds stated that they taught the rules of the game. The researchers interpreted their results as indicating a "shift in children's understanding of teaching – from focusing on behavioral aspects to appreciating the mental states involved, specifically knowledge and understanding" (p. 1484). Such a shift between the age of three and five might reflect the development of theory of mind abilities. Both Strauss and colleagues (2002) and Davis-Unger and Carlson (2008) related the increase in teaching strategies between the age of 3 and 5 to a simultaneous increase in the ability to solve theory of mind tasks. This correlation was significant even after controlling for age (Davis-Unger & Carlson, 2008) and suggests that as children become more able to identify false beliefs in others, they also become more able to teach in an increasingly adapted manner. By taking into account the mental state of the partner, children might become more receptive to errors made and ask questions to assess whether learning has occurred.

The skills of teaching are nevertheless still limited and "contingent instruction" – teaching that is tailored to the skill level and thus reduced upon recognizing that the partner acquired certain steps of the skill – develops somewhat later (Wood, Wood, Ainsworth, & O'Malley, 1995). Ziv, Solomon, Strauss, and Frye (2016) found that already 5- in comparison to 4- and 3-year-olds start to integrate the changing knowledge state of their partner. This replicates Strauss and colleagues (2002) finding that 5-year-olds but not 3-year-olds started to be responsive to errors of the partner. Nevertheless, an increase in sophistication and understanding that knowledge states change over time seems to emerge only by the *age of seven* (Wood et al., 1995). Wood and colleagues (1995) related this to the emergence of second-order, or recursive, theory of mind abilities (i.e. the subject's understanding about person A's belief of person B's belief). The specific age at which second-order theory of mind abilities emerge is somewhat debated. Some studies suggest that children as young as five years can solve these tasks, while others suggest that it only emerges by the age of six or later (Miller, 2009). Miller (2009) argued that such differences are due to the general approach taken by researchers. Studies that asked children about A's belief of B's mental state tend to find that children from an age of six to seven became able to answer correctly. However, studies that asked children about A's intent to manipulate B's mental state tend to find that children already from an age of five became able to solve them. It seems that "the distinction, thus, is between A *thinks* that B… and A *intends* that B…" (Miller, 2009, p. 752). This corroborates Ziv and colleagues (2016) finding that understanding intentions behind another person's teaching influenced whether children used contingent teaching, independent of the child's age and language level. In their study, children were more likely to adapt their own teaching to the partner's changes in knowledge if they could perceive intentionality behind the teaching of others (e.g. games can be used to teach, and individuals can engage in teaching even though no learning takes place on part of the pupil). Therefore, increased sophistication of contingent teaching around the age of seven possibly reflects the development of understanding not only second-order intentions but also second-order beliefs around the age of six. Nevertheless, the relationship between the two cognitive abilities is still unknown and we do yet not know whether theory of mind abilities and teaching skills co-develop or support each other causally.

Ludeke and Hartup (1983) showed that *9- and 11-year-olds* most frequently used rule statements, repetitions of rules, and demonstrations to teach others. They also gave strategic advice ("information about advantageous response alternatives") and called attention to the game materials or the own actions. Nine-year-olds more than 11-year-olds directly assisted their same-aged partners by intervening into their actions and assessed the partner's ability through questions. Yet, the rate increased for both variables when teachers of each age group were paired with younger partners (i.e. 11-year-old teachers: 9- and 7-year-old partners; 9-year-old teachers: 7-year-old partners). Both age groups showed a significant increase in repeating rules and 11-year-olds also gave more strategic advice when paired with younger partners than same aged partners. Children of both age groups did not frequently give supportive feedback such as praise, except when 11-year-olds taught 7-year-olds. Therefore, it seems that only a great difference in age to their pupil led 11-year-old teachers to give praise during teaching instances. The difference in teaching strategies observed towards same-aged and younger partners could not be explained by the partner's mistakes or communication. The authors concluded that 9- and 11-year-old children seemed to possess a "theory of teaching" in that they might have understood that younger children are "cognitively limited and therefore require extra consideration in delivering information" (p. 913). Therefore, it seems that 9-year-old children not only start to rely mainly on rule statements instead of specific explanations but they additionally give strategic advice. They exhibited both strategies more often when facing younger partners than partners of their own age. Eleven-year-olds additionally praised their partner when he or she was four years younger than themselves.

Finally, Ellis and Rogoff (1982) investigated the difference between 9-year-old and *adult* teachers when paired with 7-year-old pupils. Adults provided more generalizable than specific verbal information and children showed the reverse pattern, though the difference was not significant for 9-year-olds. Overall adult teachers provided both types of verbal information more frequently than child teachers. Thus, while adults relied more on verbal instead of nonverbal information, again the reverse pattern was true for children. Given that the frequency of nonverbal information was similar between adult and child teachers, adults provided more information in total (i.e. the rate of verbal information was three times the rate of that of children). Accordingly, pupils learned better when the teacher was an adult and also performed better on subsequent tests assessing whether they memorized and generalized the learned information. The authors suggested that 9-year-olds in comparison to adults were not able to identify the zone of proximal development and consequently were less accurate while teaching.

To sum up, a clear developmental trajectory seems to emerge from the literature. Young children start to incorporate changes in knowledge state, however still identify their partner's actions as behavioural instead of mentally caused and predominantly use demonstrations instead of verbal communication. With increasing age, verbal communication during teaching episodes develops: Children seem to first use explanations followed by knowledge state assessments through directed questions, while much later they use rule statements, give strategic advice, and praise. Only adults seem to reliably provide generalizable information.

Even though the emerging picture seems intriguingly clear, we need more studies to verify these results. Several studies that assessed children between the ages three to five find similar results, however only a few studies assessed the other age groups. Additionally, the methods differ between studies and we do not know the extent to which the testing procedure influences results. This adds difficulty when comparing teaching strategies across studies to derive conclusions about the developmental trajectory of such. Furthermore, even though we know that young children help with other-regarding intentions, we are currently lacking research on the underlying motivations of teaching and how it influences which strategies children use. In most studies, children are directly asked to teach the new partner, which not only primes them to engage in what they perceive to be teaching through previous interactions, but also places external pressure from an adult experimenter on the likelihood that they will. Both factors might influence whether and which strategies are used and distort our assumption of how teaching might occur in naturalistic settings.

We therefore sought to address some of the limitations discussed above. To analyse the ontogenetic development of pedagogical capabilities, we tested children from 4 to 7 years. We could not include 3-year-olds because they did not pass training, so the youngest subjects were 3.5 years old. Nonetheless, our age range entails the developmental sequence in which most growth in terms of acquiring sophisticated teaching skills seems to occur. The age difference between teacher and pupil was maximally six months to rule out changes in communication styles due to an age gap (e.g. Ludeke & Hartup, 1983; Shatz & Gelman, 1973). Using the same design for all age groups enabled us to directly compare differences in teaching strategies. Furthermore, we incorporated two tasks that only varied in whether the subject gained a benefit from teaching or not, which allowed us to infer the underlying motivation of teaching and its effect on the strategies that were employed. Children were not prompted to teach by the experimenter. Moreover, to minimize the influence of an adult's presence, the experimenter left the room after introducing the game and only a second but seemingly distracted experimenter remained in the back of the room.

We used a between subject design and tested children in dyads (except in the control condition 'Empty'). In each dyad, we assigned one child the role of the "demonstrator" and the other child the role of the "observer". The demonstrator was trained to operate an apparatus by pulling and turning a handle. In the test, two apparatuses were placed on two tables and a transparent barrier separated both tables to ensure that children could see but not walk to the other desk. In experiment 'Independent', both children received the same apparatus and both apparatuses provided rewards to the operating individual. Therefore, both children could retrieve rewards with their own apparatus independently of the other child. In experiment 'Dependent', we presented the demonstrator with a functional but empty apparatus of the same type as we used in experiment 'Independent'. Given that in this experiment the apparatus remained empty throughout the entire test, the demonstrator could not obtain rewards by him- or herself. The observer, however, was presented with an identical apparatus that simultaneously produced rewards to the acting observer and the demonstrator via a long slide. Therefore, to acquire any rewards the demonstrator was now dependent on the skill of the observer.

We ran four conditions, one test and three control conditions. In the test condition 'Naïve', the observer was a naïve child that had never seen the apparatus before. We investigated 1) whether the trained child would start to demonstrate or explain the mechanism, 2) the means used to teach (demonstrating with the own apparatus, using gestures, verbal communication), 3) whether the strategies used depended on the age of the demonstrator, and 4) the motivations that underlay teaching (experiment 'Independent' vs 'Dependent'). We used motion trackers to identify even subtle changes in movements performed on the apparatuses of both children of each dyad. To rule out different alternative explanations of why the demonstrator might have started to teach, we included three control conditions. In the control condition 'Empty', the demonstrator was alone and we assessed the baseline level of how children behaved when no audience was present. In the control condition 'Social Facilitation', a naïve child was present but sat on the opposite side of the demonstrator and therefore was not able to manipulate an apparatus herself. This control condition helped to gauge whether children started to teach just because another child was present and irrespective of whether that child actually needed information. Finally, in the control condition 'Expert' the partner sat in front of the second apparatus - as the naïve partner did in the test condition - but she was also trained prior to the test. We used this control condition to assess how children behaved when another individual was present who had access to the apparatus but did not need help.

Based on the existing literature, we expected younger children to rely more on physical means and demonstrate actions on their own apparatus. With increasing age we expected that children would use more iconic gestures that would be later superseded by verbal communication, such as giving feedback or explained the game more generally. We expected that children of all age groups would give specific explanations to convey how the apparatus functions and would draw attention to themselves or the task.

B. Methods

1. Ethical Note

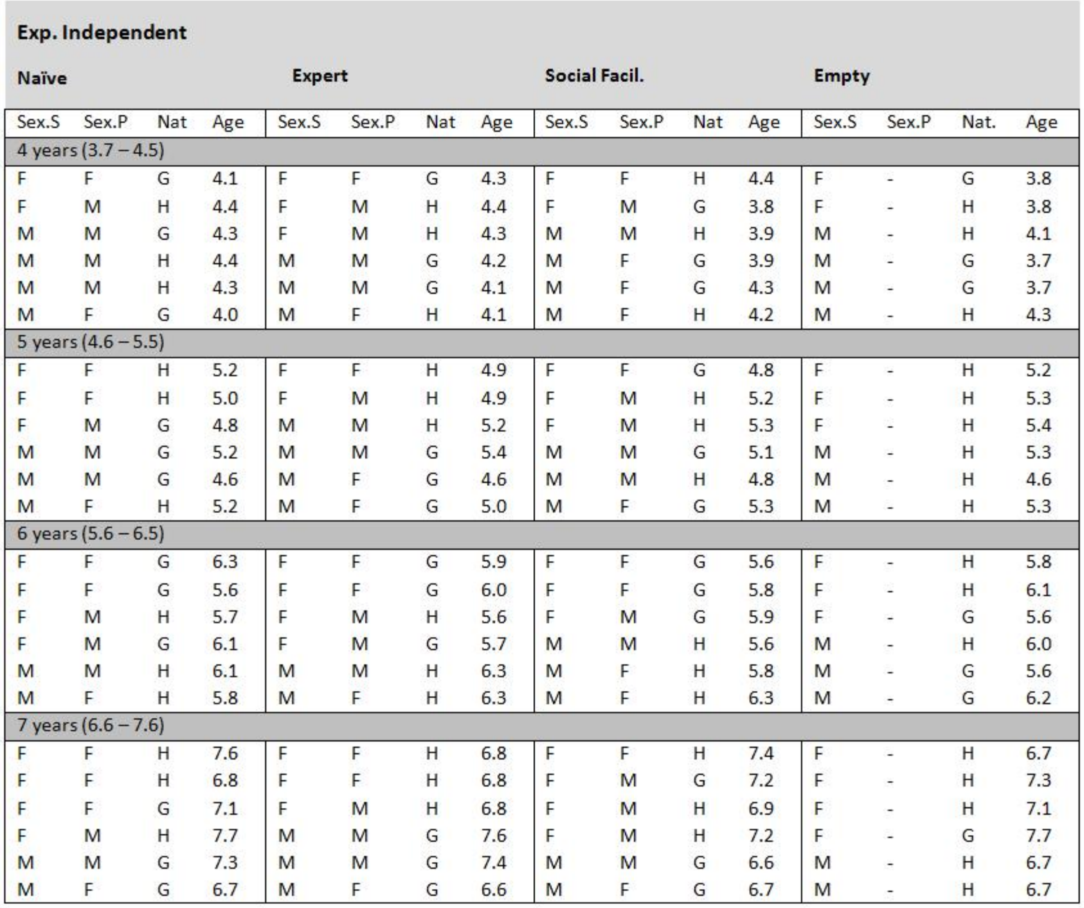
For all Hungarian subjects, parents or legal guardians gave their consent to the Central European University (CEU) to conduct behavioural studies with their children. For all German subjects, parents or legal guardians gave their consent to the Max Planck Institute for Evolutionary Anthropology (MPI). Before signing the consent forms and before the experiment started, we disclosed the entire procedure to the respective parents, guardians, or caretakers. They knew that they could withdraw the child's participation in the test at any moment. Given that we could not disclose the entire procedure to the children, we asked if they wanted to play a game with us and conveyed roughly what was going to happen without communicating anything about the task itself. Thus, we stated that they could play a game during which they could collect "Kinder Surprise Eggs" and exchange them for stickers. Moreover, we stated that later on they might play with another child. If they did not want to join, this was completely fine.

2. Subjects

Subjects were 192 four- to seven-year-old children (age range of 3.5 to 7.8 years; 96 boys and 96 girls; see Table 4.1). We tested children from several different populations: Visiting children at the Zoo and Botanical Garten Budapest, Hungary, children at various kindergartens and after school day cares in Budapest, and children at various kindergartens and after school day cares in Leipzig, Germany. Research assistants recruited children visiting the Gyermek Labor within the zoo in Budapest and asked if they would like to participate in the study. Children tested at kindergartens and after school day cares were recruited by responsible coordinators at CEU or MPI. Children of each dyad were familiar with each other as they were from the same group visiting the zoo or in the same kindergarten and after school day care. We, however, did not take a formal measure of the specific relationship between the partners.

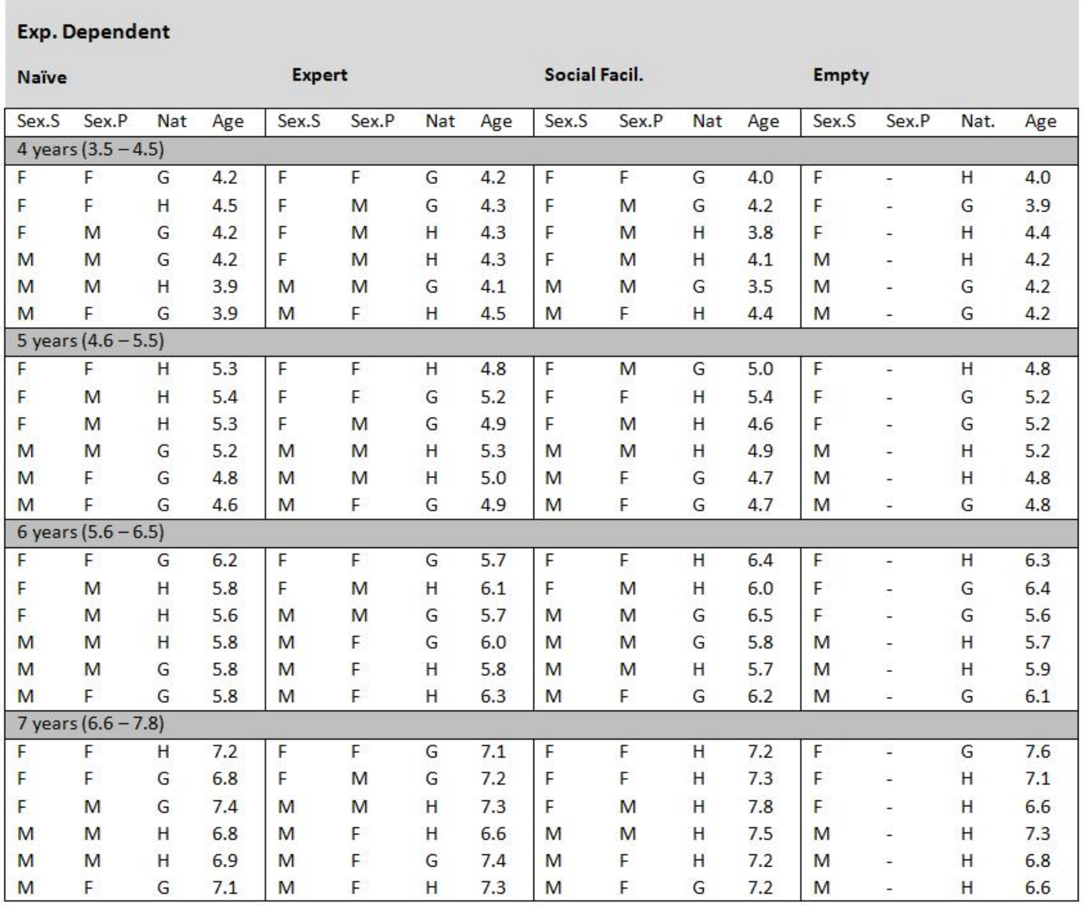
In each dyad, the age difference between the subject and her partner was maximally six months. In each combination of age group and condition, we tested six children. For each of these six children, we included one male-male, one female-female, one male-female, and one female-male pair (see Table 4.1). We added the remaining two subjects in a way to achieve roughly the same amount of sex-combinations within each condition. Moreover, three of the six children in each condition and experiment were German and the remaining three were Hungarian (for few exceptions see Table 4.1). The German children were tested by the first author and the Hungarian children were tested by Iulia Savos, a research assistant at CEU.

Table 4.1 Subject list of experiment 'Independent' and 'Dependent' listing the sex of the subject (Sex.S) and the partner (Sex.P), the Nationality of both, and the age of the subject. The age of the partner was always maximally six months younger or older.



Exp. Independent

Naïve				Expert				Social Facil.				Empty			
Sex.S	Sex.P	Nat	Age	Sex.S	Sex.P	Nat	Age	Sex.S	Sex.P	Nat	Age	Sex.S	Sex.P	Nat.	Age
4 years (3.7 – 4.5)															
F	F	G	4.1	F	F	G	4.3	F	F	H	4.4	F	-	G	3.8
F	M	H	4.4	F	M	H	4.4	F	M	G	3.8	F	-	H	3.8
M	M	G	4.3	F	M	H	4.3	M	M	H	3.9	M	-	H	4.1
M	M	H	4.4	M	M	G	4.2	M	F	G	3.9	M	-	G	3.7
M	M	H	4.3	M	M	G	4.1	M	F	G	4.3	M	-	G	3.7
M	F	G	4.0	M	F	H	4.1	M	F	H	4.2	M	-	H	4.3
5 years (4.6 – 5.5)															
F	F	H	5.2	F	F	H	4.9	F	F	G	4.8	F	-	H	5.2
F	F	H	5.0	F	M	H	4.9	F	M	H	5.2	F	-	H	5.3
F	M	G	4.8	M	M	H	5.2	F	M	H	5.3	F	-	H	5.4
M	M	G	5.2	M	M	G	5.4	M	M	G	5.1	M	-	H	5.3
M	M	G	4.6	M	F	G	4.6	M	M	H	4.8	M	-	H	4.6
M	F	H	5.2	M	F	G	5.0	M	F	G	5.3	M	-	H	5.3
6 years (5.6 – 6.5)															
F	F	G	6.3	F	F	G	5.9	F	F	G	5.6	F	-	H	5.8
F	F	G	5.6	F	F	G	6.0	F	F	G	5.8	F	-	H	6.1
F	M	H	5.7	F	M	H	5.6	F	M	G	5.9	F	-	G	5.6
F	M	G	6.1	F	M	G	5.7	M	M	H	5.6	M	-	H	6.0
M	M	H	6.1	M	M	H	6.3	M	F	H	5.8	M	-	G	5.6
M	F	H	5.8	M	F	H	6.3	M	F	H	6.3	M	-	G	6.2
7 years (6.6 – 7.6)															
F	F	H	7.6	F	F	H	6.8	F	F	H	7.4	F	-	H	6.7
F	F	H	6.8	F	F	H	6.8	F	M	G	7.2	F	-	H	7.3
F	F	G	7.1	F	M	H	6.8	F	M	H	6.9	F	-	H	7.1
F	M	H	7.7	M	M	G	7.6	F	M	H	7.2	F	-	G	7.7
M	M	G	7.3	M	M	G	7.4	M	M	G	6.6	M	-	H	6.7
M	F	G	6.7	M	F	G	6.6	M	F	G	6.7	M	-	H	6.7



Exp. Dependent															
Naïve				Expert				Social Facil.				Empty			
Sex.S	Sex.P	Nat	Age	Sex.S	Sex.P	Nat	Age	Sex.S	Sex.P	Nat	Age	Sex.S	Sex.P	Nat.	Age
4 years (3.5 – 4.5)															
F	F	G	4.2	F	F	G	4.2	F	F	G	4.0	F	-	H	4.0
F	F	H	4.5	F	M	G	4.3	F	M	G	4.2	F	-	G	3.9
F	M	G	4.2	F	M	H	4.3	F	M	H	3.8	F	-	H	4.4
M	M	G	4.2	F	M	H	4.3	F	M	H	4.1	M	-	H	4.2
M	M	H	3.9	M	M	G	4.1	M	M	G	3.5	M	-	G	4.2
M	F	G	3.9	M	F	H	4.5	M	F	H	4.4	M	-	G	4.2
5 years (4.6 – 5.5)															
F	F	H	5.3	F	F	H	4.8	F	M	G	5.0	F	-	H	4.8
F	M	H	5.4	F	F	G	5.2	F	F	H	5.4	F	-	G	5.2
F	M	H	5.3	F	M	G	4.9	F	M	H	4.6	F	-	G	5.2
M	M	G	5.2	M	M	H	5.3	M	M	H	4.9	M	-	H	5.2
M	F	G	4.8	M	M	H	5.0	M	F	G	4.7	M	-	H	4.8
M	F	G	4.6	M	F	G	4.9	M	F	G	4.7	M	-	G	4.8
6 years (5.6 – 6.5)															
F	F	G	6.2	F	F	G	5.7	F	F	H	6.4	F	-	H	6.3
F	M	H	5.8	F	M	H	6.1	F	M	H	6.0	F	-	G	6.4
F	M	H	5.6	M	M	G	5.7	M	M	G	6.5	F	-	G	5.6
M	M	H	5.8	M	F	G	6.0	M	M	G	5.8	M	-	H	5.7
M	M	G	5.8	M	F	H	5.8	M	M	H	5.7	M	-	H	5.9
M	F	G	5.8	M	F	H	6.3	M	F	G	6.2	M	-	G	6.1
7 years (6.6 – 7.8)															
F	F	H	7.2	F	F	G	7.1	F	F	H	7.2	F	-	G	7.6
F	F	G	6.8	F	M	G	7.2	F	F	H	7.3	F	-	H	7.1
F	M	G	7.4	M	M	H	7.3	F	M	H	7.8	F	-	H	6.6
M	M	H	6.8	M	F	H	6.6	M	M	H	7.5	M	-	H	7.3
M	M	H	6.9	M	F	G	7.4	M	F	H	7.2	M	-	H	6.8
M	F	G	7.1	M	F	H	7.3	M	F	G	7.2	M	-	H	6.6

3. Apparatuses

We duplicated the three apparatuses used for the chimpanzees (see Chapter 3, section B2; p. 93) and slightly adjusted their build and appearance to be safe and more appealing to children (see Figure 4.1). Hence, we again used two duplicate apparatuses to which only one magazine with ten eggs could be attached ('apparatus single') and one apparatus to which two magazines could be attached ('apparatus double'). In experiment 'Independent', we used two apparatuses of the type 'single', while in experiment 'Dependent' we used one apparatus of the type 'single' and 'double'. The respective set of apparatuses was placed on two tables with a size of 50cm height, 50cm width, and 60cm length. We positioned the tables in a way that the handles of the two apparatuses were at the same distance as they had been for the chimpanzees of the big group (i.e. 115cm apart). We used a transparent barrier with a height of 110cm and a length of 60cm that we placed between the two tables (see Figure 4.2) to prevent the children from touching the apparatus of their partner. One end of the barrier was placed against the wall of the respective room and the other end was positioned between the two tables. This created two compartments, in which the children could sit on their chairs and operate their apparatus. The space from the edge of the table to the wall was always 85cm. The handle and rod were made out of wood instead of metal and plastic but the size and internal measurements of each apparatus stayed exactly the same. Moreover, the movements that had to be performed in order to acquire an egg also stayed the same: The handle first had to be pulled by 6.5 to 7.5 cm and subsequently turned by roughly 100° in either direction. This caused the egg to drop onto the slide and roll towards the actor, where the egg could be picked up (see Figure 4.1A). When operating 'apparatus double', a second egg simultaneously dropped down a second slide and rolled into a box underneath the table of our subject (see Figure 4.1B).

Even though the mechanism remained the same, we slightly adjusted the internal parts of the apparatuses. We removed the springs and elastic band and replaced these by a weight (1kg or 0.5kg for four-year-olds) that we attached to the rod by a thin rope. The weight fulfilled the same function as the springs in that it pulled back the rod to its original position as soon as the child released the handle. The rope also fulfilled the same function as the elastic band given that it wrapped around the rod whenever the child turned the handle in either direction. Once the handle was released, the weight pushed down and unfurled the rope again, thereby turning the rod to its original position. These two mechanisms ensured that an egg could automatically drop down into the cavity (or cavities) in the rod once the child successfully retrieved an egg and released the handle. While the eggs of the chimpanzees were baited with food items, the eggs of the children remained empty. During the instruction the children learned that they could exchange any collected eggs for stickers after the test. We used a round tube with a height of 50cm and a diameter of 3cm that we positioned next to the child and in which they could store the eggs until the task was finished (Figure 4.1B). Eleven eggs could be stored in each tube by stacking them and colourful circles on the tube marked every three eggs that were stacked upon each other.

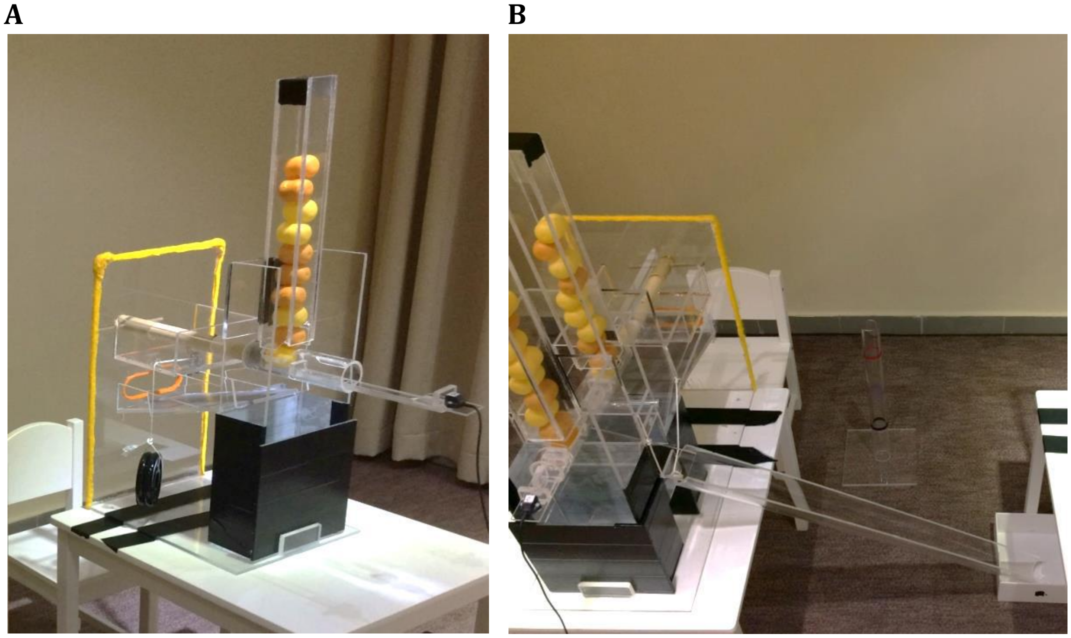


Figure 4.1 The experimenter's view of 'apparatus single' (A), and 'apparatus double' (B). The round tube, visible in picture B on the right hand side of the table, was used for children to store their eggs while playing the game.

Figure 4.2 Set-up of experiment 'Independent'. The same was used for experiment 'Dependent' but with 'apparatus double' instead of 'apparatus single' placed on the left table.

4. Design

This study entailed two different experiments. In experiment 'Independent', teaching did not result in a direct benefit for the subject and in experiment 'Dependent' the subject could only acquire rewards when the partner successfully operated her own apparatus. We used a between-subject design, hence each child only participated in one condition of one experiment. The parents, guardians, or caretakers stayed outside of the testing room for the entire study.

4.1. Training

As with the chimpanzees, the training was divided into three distinct phases (i.e. solitary exploration, shaping, and final assessment). Since we could not test the children multiple times, we had to slightly adapt the design and administered all three training phases right after one another. After the guardians and the child agreed to partake in the study, the experimenter (hereafter, E1) led the child to the apparatus on the left side, which we used for training. To reduce the possibility that the child had acquired any knowledge about this experiment through external means, we asked each child before starting the training: "Have you ever heard of this egg-machine?".

Only if this was negated, E1 continued and said: "You can sit on this chair. Today we are going to play with our egg-machine. You can collect these eggs with the machine, which you can put into this tube. In the end, you can exchange the eggs that you collected for stickers over there [points to stickers]. In order to get the eggs, you can use this wooden handle. If the eggs fall into this black box, they are unfortunately gone. But if they fall towards the front here, you can pick them up and put them into the tube. Try whether you can find out how to collect all the eggs. I have something to do over there but you can start playing, I will come back". E1 then walked to the back of the room and pretended to be busy. This training-phase was called 'Solitary exploration' and as with the chimpanzees used to assess whether children could already retrieve eggs without any further explanations about the mechanism itself. If the child asked how the apparatus worked, E1 only said: "Just try, I'll come over soon". In case, the child already successfully retrieved eggs on eight out of ten trials (80%) in this phase, she transferred into the test without completing the two additional training phases Out of the children that we included as subjects or trained partners, 25 immediately passed into the test because they gathered 80% or more of the eggs without help. The mean age of these children was 6.4 years. In case the child lost eggs on more than eight out of ten trials, after three minutes were over, or when the child did not operate the apparatus for one minute, E1 walked over to the child and started the next training phase.

The second phase, called 'Shaping', started by the experimenter saying: "Yes, this is very difficult but let's do it together. Look here, I'm taking the weight down and then it's easier". E1 took off the weight while E2 attached refilled magazine(s) to the apparatus. E1 then put the lid on top of the apparatus, placed the screw into the wooden rod (Figure 4.3) and said: "Now try again". If the child retrieved an egg, E1 said: "Well done!". In experiment "Dependent" she added: "Look a second egg rolled down this slide and into the box. If you want you can go and pick it up". If the child was repeatedly trying to turn the handle and did not try different movements, E1 asked: "What else can you do with the handle?". This was done to motivate the child to explore different possibilities. E1 never explained how the mechanism of the apparatus worked and never used any words that were related to its function. However, she could shift the attention of the children by saying "Ah!" and "Yes!" in case they were doing something correct. If an egg was lost, she said: "Oh it's gone, but just try again". E1 only blocked the turning according to a standardized schema (see Figure 4.4). If the child managed to retrieve eggs in four out of the last six trials (66%) without the turning blocked, she transferred into the last phase of training during which the weights were attached again and the apparatus was intact.

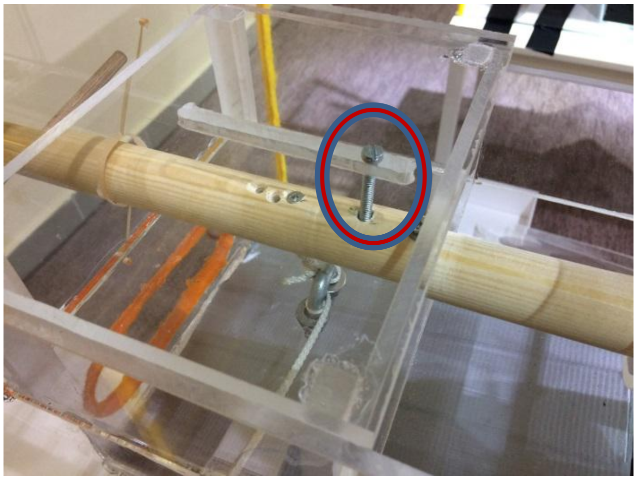


Figure 4.3 Srew and lid (highlighted by red circle) used during the training phase 'Shaping'.

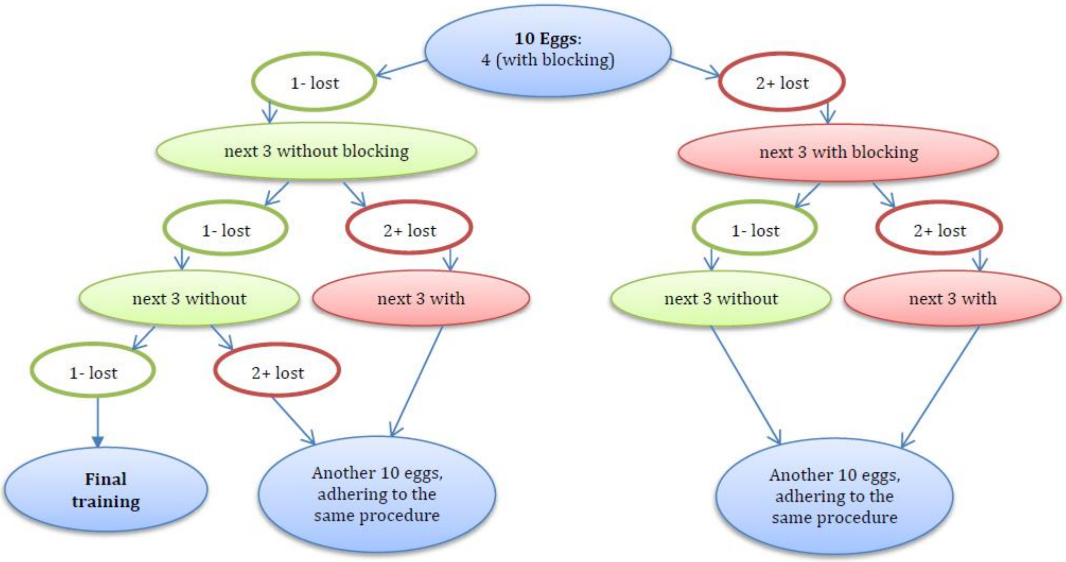


Figure 4.4 Standardized procedure of the training 'Shaping'. During this training the experimenter unblocked or blocked the handle so that the child was not able to turn it depending on the number of eggs lost. A maximum of 20 eggs were administered in this way. If the child did not reach the criterion by then, she failed the training and was not tested.

The third and final phase of training assessed whether the child was able to perform the correct actions without getting any help and while using an intact apparatus. E2 attached refilled magazine(s) to the apparatus while E1 attached the weight, took off the lid, and said: "Well done! Now it's a little harder again but you will definitely manage. Now try again". The child passed into the test if she successfully retrieved eggs on eight out of ten trials (80%) within a time limit of three minutes. In case the child already retrieved eggs on the first four out of five trials (80%), she could pass into the test immediately without having to complete the final five trials. In both cases E1 said: "Well done! Let's go to the desk with the stickers and you can pick one of them". In case the child lost eggs on three or more trials, the child did not transfer to the test and could collect three stickers immediately. Before this child was brought back to the guardians or group E1 told her: "This is our secret ok? Don't tell any of the other children about the apparatus, only we can know this secret". Subsequently, we started training the next child.

In total, 99 children that should have participated as either our subject or the trained partner did not pass the training during either the shaping or final phase.

The mean age of these children was 4.6 years (45.5% of 4-year-olds that we tried to train did not pass).

4.2. Test – Experiment 'Independent'

In the test, the subject sat at the right table and depending on the condition a second child was brought into the testing room or the subject was tested alone. We placed two duplicates of 'apparatus single' on the left and the right table and attached a magazine that contained ten eggs to both. Therefore, the subject could retrieve her own eggs independent of the partner and no direct benefits resulted from teaching. We placed a barrier between the two tables in order to prevent the subject from walking over and operating the apparatus located on the left table. One empty tube was placed next to the inner side of each table and allowed children to store their acquired eggs during the test. We incorporated four different conditions: One test and three control conditions.

In the test *condition "Naïve"*, a second child who had no knowledge of the apparatuses entered the room and sat down at the left table. When both children sat on their respective chairs, E1 introduced E2, who wore headphones, by saying: "This is …, she will have to prepare something important now and cannot hear you". E2 smiled at the children and pretended to be busy. Subsequently, E1 introduced the test and said: "You can put the collected eggs in this tube and exchange them for stickers later on. And you can put your eggs into that tube and exchange them for stickers. The rules of the game are that you stay in your compartment [performs a circular motion with the hands to highlight both areas]. Oh, there is an important phone call that I have to answer [looks at the mobile seemingly startled]. I will be back soon, you can already start". E1 left the room while E2 remained at the back of the room and pretended to be busy. In case children tried to talk to her she ignored them. In case children started to walk around the open side of their table, E2 pointed to their chair and made sure they sat down again. In case the apparatus suddenly malfunctioned and an egg got stuck while it dropped down into the cavity of the rod, E2 quickly stood up and readjusted the egg without establishing eye contact or talking to the children.

In the control *condition "Expert"*, we trained one child and after successful completion asked her to play outside while we trained a second child. The second child acted as the subject in order to keep the time elapsed between training and test the same across conditions. Once the second child successfully completed the training, E1 called in the first child and guided it to the left table. The procedure and sentences used by E1 remained exactly the same as in the test condition "Naïve". We incorporated this condition to control for any influences of the presence of another child that operated the second apparatus. Thus, we could understand if children already started to teach just because another child operated the second apparatus without taking into account the knowledge state of their partner.

In the control *condition "Social Facilitation"*, we brought a naïve child into the room but asked the child to sit down onto a chair on the right hand side of the subject instead of sitting down at the left table as in the other conditions. Before the partner entered the room, E1 told her without the subject hearing it: "You have a very important task today, please look closely at what the other child is doing". This was done to ensure that the partner remained focused on the subject, which resembled the test condition. The distance between the two chairs remained the same as the distance between the chair at the left and right table (i.e. 115 cm). We did not place a second barrier in between the two children given that there was no apparatus in front of the partner and we did not want to make the subject feel uncomfortable because each side would have been closed off by the table, wall, and barriers. The procedure and sentences used by E1 remained exactly the same as in the test condition "Naïve". We used this condition to control for any influences of the mere presence of another naïve individual. It allowed us to assess whether children already started teaching even though there was no need for the partner to learn how the apparatus worked. Thus, we could assess whether children might have started teaching due to other reasons than prosocial intent. We did not incorporate this condition for the chimpanzees because we did not have to control for the fact that they could verbally explain the procedure while manipulating the apparatus themselves. Thus, condition "Expert" and "Empty" were sufficient to control for any differences in movements that the chimpanzee subjects made as a function of the presence or absence of another individual.

In the control *condition "Empty"*, we did not ask a second child to join. Therefore, we guided the subject to the right table, while the left table remained unoccupied. We nevertheless placed the second 'apparatus single' on the left table, attached a full magazine to it, and placed the barrier between the two tables. The procedure and sentences used by E1 remained the same as in the test condition "Naïve", except for a slight adjustment to keep them natural. Instead of introducing both tubes and compartments, E1 only referred to the subject's objects and said: "You can put the collected eggs in this tube and exchange them for stickers later on. The rules of the game are that you stay in your compartment [performs a circular motion with the hand to highlight the right area]. Oh, I have an important phone call that I have to answer [looks at the mobile seemingly startled]. I will be back soon, you can already start". We incorporated this condition to acquire a baseline measure of how children behaved when no other individual except E2 was present.

Given that we used a between-subject design, each subject was only tested in one session of one condition. The session lasted three minutes, until the eggs of the subject were either retrieved or lost (condition "Empty" and "Social Facilitation"), or until the eggs of the subject's partner were either retrieved or lost (condition "Naïve" and "Expert"). Each subject and their expert partners could select two additional stickers after the test was completed and naïve partners could select three stickers since they did not receive one sticker during training. Before the children were brought back to the guardians or group E1 told them: "This is our secret ok? Don't tell any of the other children about the apparatus, only we can know this secret".

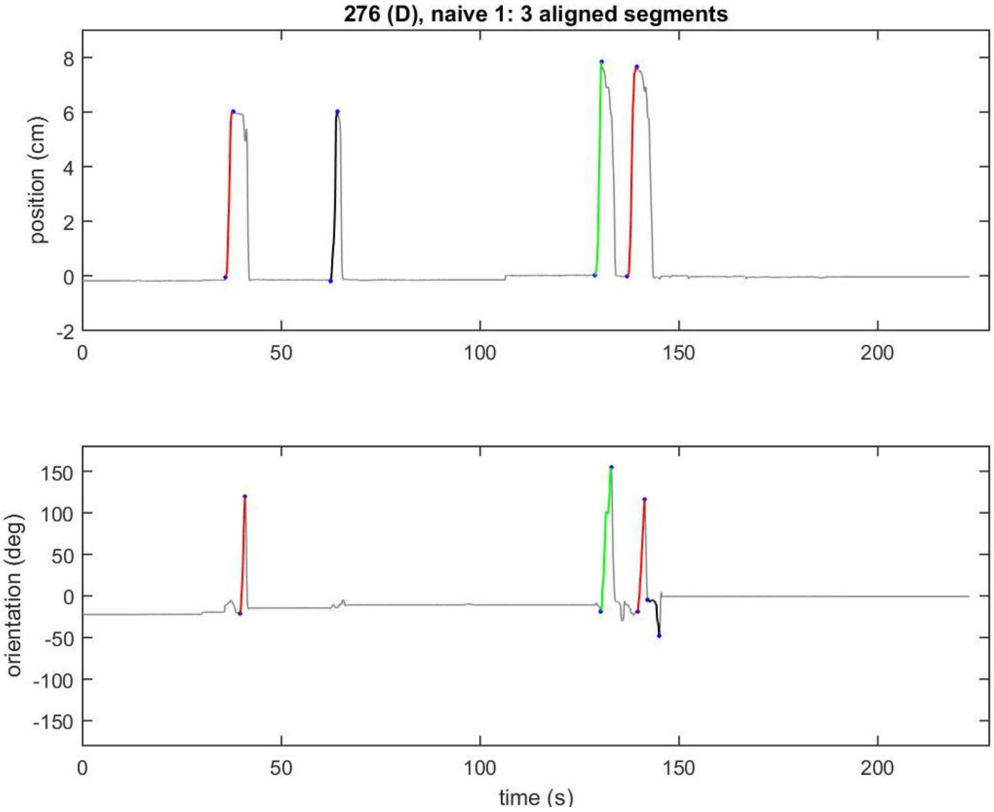
4.3. Test – Experiment 'Dependent'

In experiment 'Dependent', we trained the child to use 'apparatus double' so that she experienced that two eggs could be simultaneously retrieved. The second egg slid into a box next to the right table via a long slide. In the test, we placed 'apparatus double' on the left table and, as in experiment 'Independent', 'apparatus single' on the right table. Two magazines containing each ten eggs were attached to 'apparatus double' and no magazine was attached to 'apparatus single'. Therefore, in order to receive any eggs the subject was dependent on the success of the partner, who could operate 'apparatus double'. This resulted in a direct benefit for the subject to teach the correct actions. We placed a transparent barrier between the two tables to prevent the subject from walking over and operating 'apparatus double'. We included the same four conditions as in experiment 'Independent' for the same reasons. A session lasted three minutes or until the eggs of the subject's partner were either retrieved or lost. The entire procedure remained the same as in experiment 'Independent', except that before the second child arrived at the testing room E1 said to the subject: "The eggs that fall into this box are yours and you can pick them up". This was done to ensure that subjects knew they were allowed to collect the eggs falling into the box. Comparing the two experiments thus allowed us to investigate whether teaching was more likely to occur when there was a self-benefit instead of being done out of prosocial intent. Moreover, this procedure allowed us to assess how teaching strategies changed depending on the underlying motivation.

5. Data Coding

As for the chimpanzees, we used a Polhemus G4 motion tracking system, which captured the exact movements that each individual performed on their respective apparatus with a constant sampling rate of 120 Hz. The data was recorded by Matlab (2015) that we ran on an Asus computer with Microsoft Windows 8.1 as the operating system. We used two Polhemus hubs that each created a magnetic field, in which the exact position of the sensors could be tracked. To both apparatuses we attached one sensor to the rear end of the rod that connected to the handle. The sensors were linked to the Polhemus tracking system, which captured the data and sent it to the computer. Therefore, any changes in the sensors' position were recorded in real-time and stored for analysis. We recorded all horizontal movements (i.e. pulling) and any rotation (i.e. turning) performed with the handle over the course of the entire three minutes of each session (see Figure 4.5). The technology allowed us to detect subtle changes in the motions performed on the respective apparatus.

A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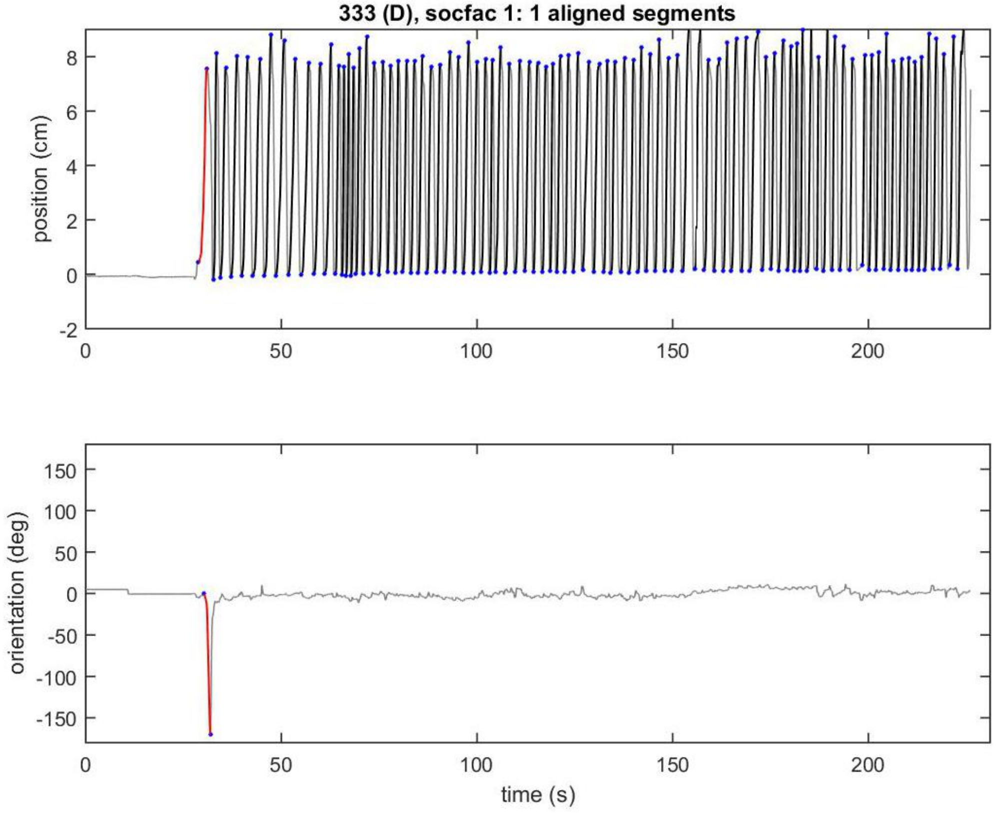
B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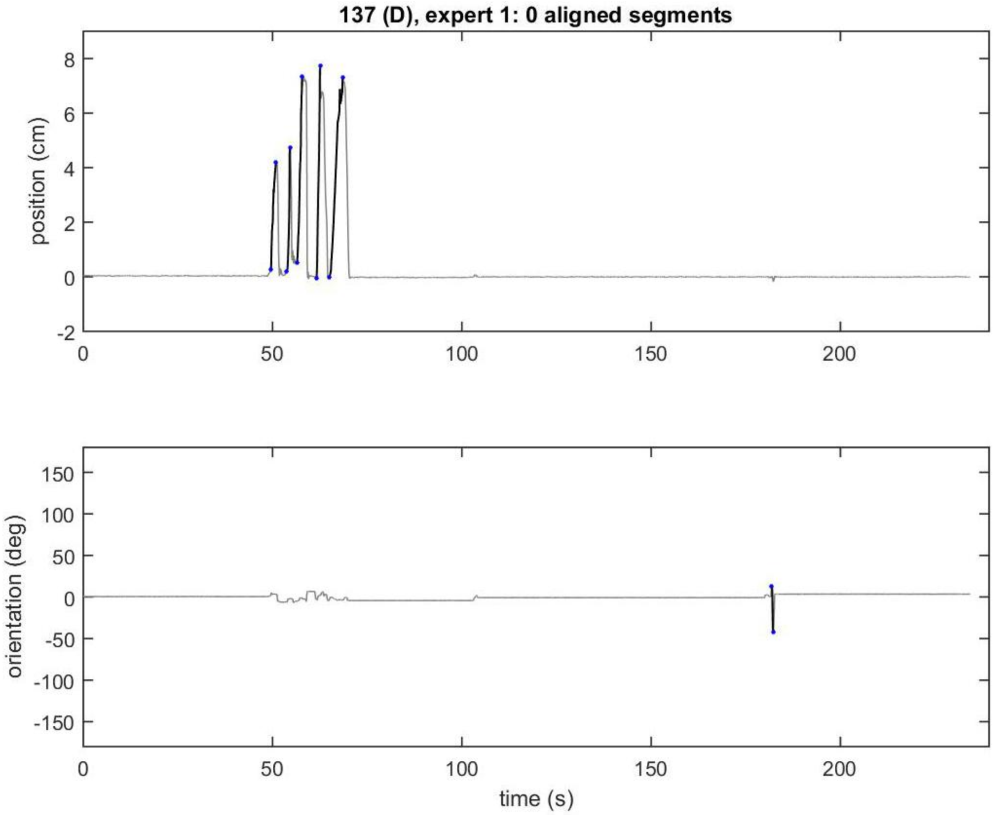

Figure 4.5 Example session of condition 'Naïve' (A), 'Social Facilitation' (B), and 'Expert' (C) in experiment 'Dependent' when the demonstrator's apparatus was empty. The top graph shows the pulling movements and the lower graph the turning movements. Rotating the handle clockwise is represented by values that have a negative sign and rotating the handle counter-clockwise is represented by positive values. Complete movements (i.e. co-occurring pulls and turns) are coloured either in red or green and the two colours alternate to enhance visibility. Incomplete movements are coloured in black. Blue dots represent the start and peak of each movement.

In addition, we coded the videos for several communicative interactions between the subject and partner. We coded whether the subject used any iconic gestures to communicate the necessary actions. Moreover, we coded whether the subject (i.e. demonstrator) verbally instructed the partner. This category was divided into the following five pedagogical subcategories:

1. Specific Explanation: Indicating how the mechanism worked (e.g. "You have to pull/turn" or "Push the handle back so that an egg falls into it") or what was necessary for acquiring an egg (e.g. "You can use both hands" or "You have to

use the handle”). This category includes all descriptions that conveyed what exactly the partner had to do in order to retrieve an egg.

2. General Explanation: Explaining the task but not directly conveying how to retrieve an egg (e.g. “If an egg falls into the black box it is gone” or “If it rolls towards here you can take it”). This category includes descriptions that alone were not sufficient to retrieve an egg. We wanted to distinguish such explanations from more specific ones, as they were helpful but only if the partner already knew what to do with the handle.
3. Feedback: Conveying whether the observer did something correct or incorrect (e.g. “Yes/No”, "No this is wrong, you have to...", "This is correct, keep doing it like this", or "Yes great").
4. Attention Getter: Getting the attention of the partner (e.g. “Here, look” or “You have to do it like this”).
5. Other: Any other verbalizations that did not fit in the other four categories.

We also coded verbalizations done by the partner (i.e. observer) and divided these into three communicative categories:

1. Questions: Any questions or active requests for help by the partner (e.g. “How does this work?” or “Can you help me”).
2. Helplessness: Any expressions of helplessness that were not necessarily directed at the subject but still conveyed that she needed help (“Oh no I lost the egg” or “I don’t know what to do”).
3. Other: Any other verbalizations that did not fit the other two categories.

We used Solomon Coder to code all of the behaviours obtained through video recordings. All non-verbal behaviours and verbal episodes of the German children were coded by the first author and verbal episodes of the Hungarian children were coded by Iulia Savos, who also conducted the testing. To assess reliability of all verbal and non-verbal variables, three research assistants who were blind to the procedure and hypotheses coded 20% of the data (39 videos). Two research assistants from CEU coded the Hungarian data, one assistant coded 20% of experiment ‘Independent’ and the second 20 % of experiment ‘Dependent’. We randomly selected the videos within each experiment. The third research assistant was from the MPI and coded 20% of the German data, randomly selected from both experiments. We calculated Cohen's Kappa for each of the three categories (i.e. iconic gestures, verbal communication of the demonstrator and verbal communication of the observer) and acquired sufficient and good reliability for each (Iconic gestures: K = 0.68; Verbalizations demonstrator: K = 0.82; Verbalizations observer: K = 0.83).

6. Data Analyses - General Information

As in the previous chapter, I will first describe the general statistical tools that we used before going into detail about the specific analyses that we performed to answer our different questions. I will discuss these analyses and the corresponding results as separate sections for the two experiments. Thus, the first section encompasses the analyses and results for the data of experiment 'Independent', and the subsequent section encompasses the analyses and results of experiment 'Dependent'. Finally, I will present the analyses and results of the comparison between the two experiments that enabled us to gauge how motivational factors changed the demonstrators' responses. The chapter closes with a section in which I will discuss all results.

All models were fitted in R (version 3.4.4; R Core Team, 2018). For the standard Poisson and binomial Generalized Linear Mixed Model (GLMM; Baayen, 2008) we used the function glmer, for the negative binomial Poisson GLMMs the function glmer.nb, for the linear mixed models (LMM; Baayen, 2008) the function lmer, and for the Generalized Linear Model (GLM; Baayen, 2008) the function glm provided by the package 'lme4' (Bates et al., 2015). Finally, for the negative binomial Poisson GLM we used the package 'MASS' (Venables & Ripley, 2002). For each model, the level of significance was set to 0.05.

To check the overall significance of the respective key predictors of the final model, we ran a maximum likelihood ratio test that compared the full model with a null model from which the key predictors were omitted (Forstmeier & Schielzeth, 2011). Only if the comparison between the full and null model reached significance did we investigate the effect of the individual key predictors. Moreover, we excluded nonsignificant interactions only when the full-null comparison was significant and in order to be able to assess the influence of the main effects.

We evaluated whether the assumptions of each model were fulfilled. For the Gaussian LMMs we visually inspected qqplots and plots of the residuals plotted against the fitted values to gauge whether the assumption of normality and homoscedasticity of the residuals were met. No obvious deviations could be detected. For each Poisson model, we ran a formal dispersion test to assess whether the model was under- or over-dispersed and adjusted the models accordingly in case the initial model was over-dispersed. To rule out collinearity, we inspected Generalized Variance Inflation Factors (GVIF; Fox & Weisberg, 2011) of all aforementioned models from which we respectively excluded the random effects and possible interactions. The function vif provided by the R package 'car' was used (Fox & Weisberg, 2011) and revealed no collinearity problem with any of our models (maximum VIF = 1.09; Zuur et al., 2010). Finally, we investigated whether the model parameters were stable and no influential cases existed in the data. We assessed whether the GLMMs and LMMs were stable by excluding the respective random effects one at a time from the data (the R-function was written by Roger Mundry and is available upon request). Comparing the model parameters with those obtained by excluding levels of the random effects one at a time showed that the model parameters were fairly stable and no influential cases existed in each of the models. With regard to the GLM, both leverage and DFBeta values indicated that no influential cases existed in the data set and that the model was fairly stable (Field, 2005; Quinn & Keough, 2002).

As was explained above, I will present the results of experiment 'Independent' before continuing to discuss the analyses of experiment 'Dependent' and the comparison between the two.

C. Experiment 'Independent' – Analyses and Results

1. Analyses

We assessed 1) which strategies the demonstrator used to teach and what factors influenced their communication, 2) whether the demonstrator used her own apparatus to teach and what factors influenced her kinematics, and 3) how the age of the demonstrator influenced the teaching strategies.

1.1. Communication

1.1.1. Difference between communication types

We first assessed how the different communication types (i.e. iconic gestures, explaining specific, explaining general, feedback, and attention getter) differed from one another and whether the demonstrators were sensitive to the fact that their help was needed in the test but not the control conditions. We fitted a GLMM with a Poisson error structure and log link function (McCullagh & Nelder, 1989) and used the count of communicative instances as our response variable. We used communicative instances as bouts and disregarded the respective total duration of each, as children might in general be differently fast in talking. We excluded children that did not talk at all including the category 'Other' (17 dyads overall). The number of observations was 275 of 55 dyads. We included an offset term (McCullagh & Nelder, 1989) to account for the fact that some children generally communicated more than others. To do this, we summed all communication types including the type 'Other' (see section B5; p. 144) that occurred within a session. This resulted in an individual number of all communicative instances, which we used to individually weigh the response variable in the model. The number of total bouts was log-transformed in order to add the offset term. We included the type of communication with five levels (Iconic gestures, Explaining specific, Explaining general, Feedback, and Attention getter) as one of our key predictors to assess whether some were exhibited significantly more frequent than others. Additionally, we used condition with three levels (Naïve, Expert, Social Facilitation) to understand whether children started teaching just because a partner was present or only when there was a need for it (i.e. in condition 'Naïve'). We did not include condition 'Empty' given that none of the measured behaviours except for 'Other' was exhibited in this condition. Finally, we included the interaction between communication type and condition to understand whether the effect of condition was different for any of the communication types. In case the interaction term is significant, it informs us that some of the behaviours (e.g. iconic gestures) were exhibited significantly more or less frequent in comparison to the other behaviours in some but not all conditions. In case the main effect but not the interaction term is significant, it informs us that some of the behaviours were exhibited significantly more or less frequent in comparison to the other behaviours but to the same degree in all conditions. These two predictors and their interaction described above were used as key predictors and added to the model as fixed effects.

As an additional fixed effect, we included the sex combination within a dyad with four levels (F-F, F-M, M-F, M-M) and the z-transformed (Ragazzini & Zadeh, 1952) variable age of the demonstrator to control for any influences that the respective sex composition or the age might have had on the number of communicative instances. To keep type 1 error rates at the nominal level of 5%, we included the random intercept (Barr et al., 2013; Forstmeier & Schielzeth, 2011) for dyad identity. We did not include random slopes components (Barr et al., 2013; Forstmeier & Schielzeth, 2011) as there was no variation within the random effect.

1.1.2. Observers' behaviour

We further wanted to understand whether children proactively communicated with their partner or whether this was driven by the behaviour of the partner. We used a binary response variable that addressed whether any of the measured communicative behaviours (i.e. iconic gestures, explaining specific, explaining general, feedback, and attention getter) was exhibited by the given subject. We fitted a GLMM with a binomial error structure and a logit link function (McCullagh & Nelder, 1989). The number of observations was 109 of 72 dyads. To understand how the behaviour of the partner influenced whether help was given, we used two predictors, called 'Questions' (i.e. all questions or active requests) and 'Helplessness' (all non-directional utterances from which the demonstrator could infer the inability of the partner). The two predictors divided the session into a maximum of three phases, which means three data points per subject: Before both of them occurred (i.e. both receive a 'No'), once either one occurs (i.e. the respective variable receives a 'Yes', while the other retains a 'No'), once the second also occurs (i.e. the second variable also receives a 'Yes', while the first retrains its 'Yes'). Through this, each subject's session was divided into a maximum of three phases with the last one indicating that both variables occurred. In case none of the two occurred, only one data point resulted for that subject (i.e. with a 'No' for both variables). To assess whether demonstrators communicated proactively or only after the partner expressed his or her inability verbally, the response indicated if any communication occurred in each of the phases. This resulted in a binary response that provided information for each phase of whether the demonstrator communicated in a relevant manner to the partner. Through this we gauged the influence that questions/active requests and utterances of helplessness had on the likelihood that the demonstrator communicated with the partner. We used an offset term to account for the different lengths of each phase. To include the offset term into the model, we log-transformed the total duration of each phase length. In addition to these two predictors, we also included the interaction between condition and the predictor 'Helplessness', as non-directional utterances might have had a different influence depending on whether the partner actually needed help. Thus, instances in which a naïve partner said "I don't know what to do" might have influenced the demonstrator differently if the naïve partner sat in front of an apparatus (condition 'Naïve') instead of on a chair without access (condition 'Social Facilitation'). We did not include the interaction between 'Questions' and condition to retain a less complex model and as these were directed at the demonstrator and should be answered to a high frequency regardless of the condition.

To control for the fact that demonstrators communicated more frequently in the test than control conditions, we included the main effect of condition with three levels (Naïve, Expert, SF). Moreover, we controlled for the influence of the demonstrator's age and the sex composition of each dyad. The variable age was z-transformed before including it in the model. The random intercept but no random slopes components (Barr et al., 2013; Forstmeier & Schielzeth, 2011) were included for dyad identity.

1.2. Kinematics

To understand whether demonstrators changed their behaviour while operating the own apparatus depending on the condition, we analysed the data collected by the Polhemus motion tracker. Four children (all tested in the social facilitation control condition) did not operate the apparatus at all and were excluded from the analyses.

1.2.1. Duration until peak

We reasoned that teaching would include slowing down, so that each movement is easier to follow for the observer. Therefore, we assessed whether the duration to reach the peak of each movement was influenced by the condition in which children were tested. To understand whether this was the case, we again fitted a LMM with a Gaussian error structure and an identity link function. The number of observations was 1916 of 92 dyads. We log-transformed our response variable (i.e. the duration to reach the peak of each movement) before including it in the model. We included the variable condition (Naïve, Expert, SF, Empty) as our predictor. Additionally, we incorporated its interactions with the age and sex of the demonstrator and with the type of movement (Pull, Turn). The first interaction term tells us whether with increasing or decreasing age children tend to slow down more in some conditions. Similarly, the second interaction term tells us whether boys or girls slowed down more than the other sex in some conditions. Finally, the third interaction term was included to assess whether children might have executed one but not both movement types slower in a given condition.

To control for the main effect of the type of movement and age and sex of the demonstrator, we included the three variables as fixed effects in the null model. Age was z-transformed before inclusion. Moreover, to control for the effect that time might have had on the behaviour of the demonstrators, we included the segment number of each movement. The variable segment number was heavily right skewed and we needed to transform it by subtracting the minimum value from each original value and taking the square root of these. We incorporated the random intercept (Barr et al., 2013; Forstmeier & Schielzeth, 2011) for subject identity, and the random slopes components (Barr et al., 2013; Forstmeier & Schielzeth, 2011) within subject identity for the type of movement and the transformed variable segment.

1.2.2. Separation of movements

Furthermore, we reasoned that teaching would also include separating the two movements to make them visually more assessable for the observer, which would result in a greater duration between the onset of the pulling movement and the onset of the turning movement. The most efficient strategy is to start turning shortly after pulling, so that both the minimal distance and minimal degree required to retrieve an egg are co-occurring. In case children are using their own apparatus to demonstrate the two movements, one way to make the movements more visible is to separate the two. This would result in a greater duration between the points in time that children started to turn once they pulled. We fitted a LMM with a Gaussian error structure and an identity link function. The number of observations was 884 of 90 dyads. Our response variable was the duration between the start of the pulling movement to the start of the turning movement of all complete movements (i.e. pulls and turns that overlapped). For a movement to be considered complete the onset of a pull movement had to occur before the peak of a turn movement, or the turn onset had to occur before the pull end. Thus, in most cases a retrieved egg resulted from complete actions. Given that the distribution of the response was skewed in both directions, we transformed it before including it in the model. We used a log-transformation of the absolute values to which we added a constant of one, and multiplied this by the reverse sign of each original value. This transformation was the only transformation that could deal with skewed data in both directions and a few negative in addition to mostly positive values. As in the previous model, we added condition with four levels (Naïve, Expert, SF, Empty) and its interaction with the age and sex of the demonstrator.

Again, as in the previous model, we included the main effect of sex and age of the demonstrator and the segment number of each movement. The variable segment number was z-transformed. We also included the random intercept (Barr et al., 2013; Forstmeier & Schielzeth, 2011) for subject identity, and the random slopes component (Barr et al., 2013; Forstmeier & Schielzeth, 2011) within subject identity for the variable segment number.

1.3. Ontogeny of strategies used

We further wanted to know how the age of the demonstrator influenced which strategy was used to communicate with the partner. We fitted a GLMM with a binomial error structure and logit link function (McCullagh & Nelder, 1989). The number of observations was 360 of 72 dyads. Our response variable indicated for each communicative type whether the given demonstrator exhibited it at least once. We used the interaction between the communicative type with five levels (Iconic gestures, Explaining specific, Explaining general, Feedback, and Attention getter) the z-transformed (Ragazzini & Zadeh, 1952) variable age of the demonstrator as the sole key predictor. The interaction term informs us whether the strategy used to communicate with the partner changed with increasing or decreasing age.

We included the main effect of the different strategies used, as we were not interested in their sole influence but only in combination with the demonstrators' age. Sex combination within a dyad with four levels (F-F, F-M, M-F, M-M) and the age of the demonstrator were included to control for any influences that the respective sex composition or the age might have had on the occurrence of communicative instances in general. Moreover, we included the type of condition with three levels (Naïve, Expert, Social Facilitation) to control for the fact that demonstrators shared generally more information in the test than control conditions.

As in the previous model, we incorporated the random intercept (Barr et al., 2013; Forstmeier & Schielzeth, 2011) for dyad identity but no random slopes components (Barr et al., 2013; Forstmeier & Schielzeth, 2011).

2. Results

2.1. Communication

2.1.1. Difference between communication types

We first scrutinized whether children exhibited the different communication types to a different degree to each other and between conditions. Figure 4.6 shows the mean number of bouts of each communicative type that children exhibited in each of the three social conditions. Across conditions, 33 out of 72 demonstrators communicated with their partners in a relevant manner. We did not observe any of the coded behaviours except for 'Other' (see section B5; p. 144) in the control condition 'Empty'. Overall, demonstrators exhibited specific explanations the most, followed by feedback, general explanations, attention getters, and iconic gestures.

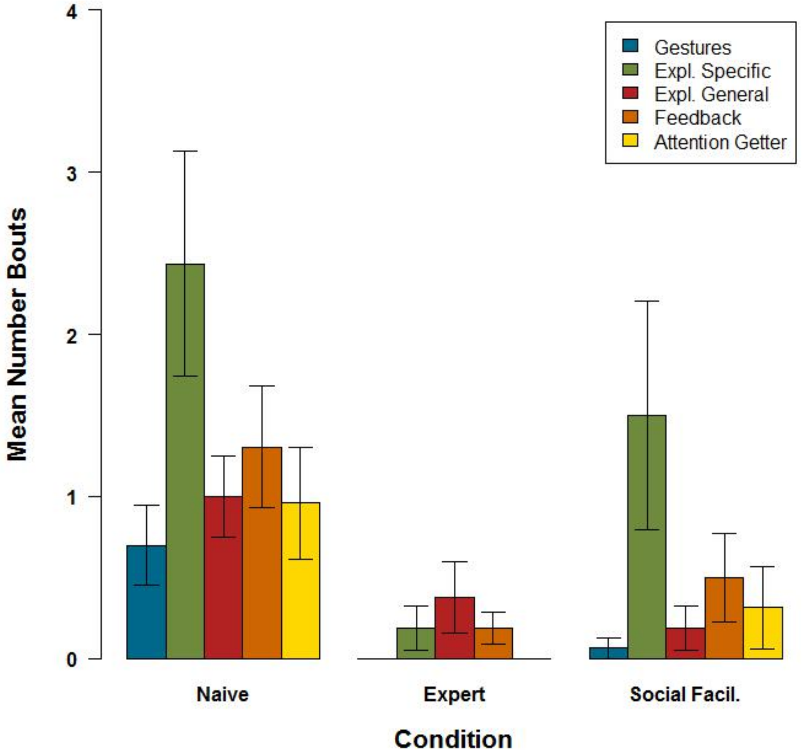

Figure 4.6 Mean number of bouts of each communicative type that children exhibited in each of the three social conditions of experiment 'Independent' and corresponding 95% confidence intervals.

The GLMM including the type of communication, condition, and the interaction between the two was significantly different to a model that did not include these predictors (χ^2 = 38.96, df = 10, N = 275, p < .001, Table 4.2). The interaction between communication type and condition was significant (χ^2 = 20.9, df = 8, p = .007). Even though children used significantly more relevant verbal and gestural communication in condition 'Naïve' compared to the control conditions, they explained the specific mechanism to a similar degree in condition 'Social Facilitation' (i.e. when the partner was naïve but could not make direct use of the information). Nevertheless, demonstrators exhibited each of the other behaviours significantly less in condition 'Social Facilitation' than condition 'Naïve'. Comparing the two social control conditions with each other shows that children exhibited significantly more specific explanations and attention getters in condition 'Social Facilitation' than in condition 'Expert'. Due to the fact that children did not use iconic gestures or attention getters in condition 'Expert', the standard errors for the associated comparisons between condition ‘Naïve’ and ‘Expert’ are very large and respective statistics have to be interpreted with caution.

Table 4.2 Results of the GLMM that assessed whether the number of bouts of each communication type was different between types and between conditions.

Term	Estimate	SE	lower CI	upper CI	χ^2	*P*
Intercept	-1.82	0.25	-2.34	-1.36	(3)	(3)
Condition						
Naïve vs Expert	-1.93	0.64	-7.58	-0.99	(3)	(3)
Naïve vs SF	-0.35	0.32	-1.09	0.24	(3)	(3)
Comm. Type						
Expl.S vs Att.Gett	-0.93	0.25	-1.53	-0.46	(3)	(3)
Expl.S vs Expl.G	-0.89	0.25	-1.46	-0.41	(3)	(3)
Expl.S vs Feedback	-0.62	0.23	-1.15	-0.2	(3)	(3)
Expl.S vs Iconic	-1.25	0.29	-1.90	-0.69	(3)	(3)
Age Dem(1)	0.02	0.12	-0.21	0.27	0.04(2)	.847(2)
Sex Comp.					0.70(2)	.873(2)
FF vs FM	0.04	0.38	-0.82	0.83	(3)	(3)
FF vs MF	0.25	0.34	-0.46	0.93	(3)	(3)
FF vs MM	0.05	0.3	-0.51	0.61	(3)	(3)
Comm.Type*Condition					20.9(2)	.007(2)
Naïve vs Expert						
Expl.S vs Att.Gett	-17.32	5467.28	-18.87	-15.38	(3)	(3)
Expl.S vs Expl.G	1.58	0.77	0.17	6.81	(3)	(3)
Expl.S vs Feedback	0.62	0.87	-6.27	5.57	(3)	(3)
Expl.S vs Iconic	-17	5450.80	-18.58	-15.15	(3)	(3)
Naïve vs SF						
Expl.S vs Att.Gett	-0.63	0.56	-2.29	0.49	(3)	(3)
Expl.S vs Expl.G	-1.19	0.67	-8.44	-0.05	(3)	(3)
Expl.S vs Feedback	-0.47	0.47	-1.58	0.49	(3)	(3)
Expl.S vs Iconic	-1.93	1.07	-8.91	-0.4	(3)	(3)

(1) standardized to its mean
(2) overall effect of the predictor
(3) not shown because of limited interpretation

2.1.2. Observers' behaviour

Furthermore, we investigated how the behaviour of the observer (i.e. direct and indirect indicators of needing help) influenced whether the demonstrator provided communicative help. Figure 4.7 indicates whether demonstrators communicated proactively or only after the partner expressed his or her inability verbally. It shows that 22 of 72 demonstrators already started to communicate in a relevant manner without the partner first directly (i.e. 'Questions') or indirectly (i.e. 'Helplessness') expressing his or her inability. Out of these, 13 demonstrators were tested in condition 'Naïve', 2 in condition 'Expert', and 7 in condition 'Social Facilitation'.

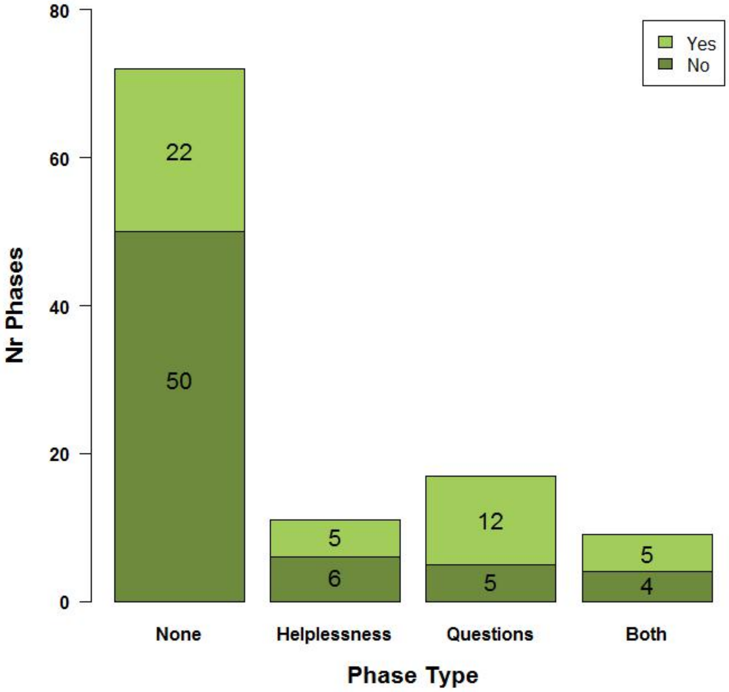

Figure 4.7 Number of different types of phases across all three social conditions in experiment 'Independent', split by phases in which the demonstrator did and did not communicate in a relevant manner. The total number of dyads is the sum of 'None' phases, given that partners never uttered questions or helplessness on second one of a session. On 22 sessions partners did not exhibit questions and helplessness before the demonstrator communicated in a relevant manner.

The GLMM that investigated the influence of direct (i.e. 'Questions') and indirect (i.e. 'Helplessness') utterances on the likelihood that the demonstrator communicated with the partner yielded a significant result (χ^2 = 9.47, *df* = 4, *N* = 109, *p* = .05). The interaction between condition and 'Helplessness' was not significant (χ^2 = 3.95, *df* = 2, *p* = .139), so we omitted it from the model to interpret the main effect of 'Helplessness'. The new model only yielded a borderline significant result in comparison to a model from which the remaining predictors 'Questions' and

‘Helplessness’ were omitted (χ^2 = 5.52, *df* = 2, *N* = 109, *p* = .063, Table 4.3). Only the predictor ‘Questions’ (χ^2 = 5.18, *df* = 1, *p* = .023) but not the predictor ‘Helplessness’ (χ^2 = 0.04, *df* = 1, *p* = .851) contributed to explaining variance in why the demonstrator communicated with the partner. Nevertheless, given that the model only reached borderline significance, more data is needed to confirm that it actually had an effect. Thus, with the current data set it seems that demonstrators were neither reactive upon hearing that the partner was helpless and nor when she directly asked for help.

Partners did not express questions or helplessness first much more frequently than the other: 11 out of 72 partners first uttered helplessness such as “I lost it” or “This is difficult”, whereas 17 partners first directly requested help through questions targeted at the demonstrator or making direct statements such as “Please explain”. Thus, the model was not influenced by a greater frequency of one type occurring first.

Table 4.3 Results of the GLMM that assessed whether the behaviour of the partner influenced the demonstrator communicating in a relevant manner.

Term	Estimate	SE	lower CI	upper CI	χ^2	*P*
Intercept	-0.38	0.72	-2	1.05	(3)	(3)
Questions No vs Yes	1.58	0.74	0.21	3.24	5.18(2)	.023(2)
Helpless No vs Yes	-0.15	0.79	-1.80	1.38	0.04(2)	.851(2)
Age Dem(1)	0.44	0.33	-0.22	1.19	1.75(2)	.186(2)
Sex Comp.					6.21(2)	.102(2)
FF vs FM	-0.12	0.96	-2.21	1.85	(3)	(3)
FF vs MF	1.28	0.95	-0.55	3.48	(3)	(3)
FF vs MM	1.75	0.93	0.06	4.03	(3)	(3)
Condition					11.32(2)	.003(2)
Naïve vs Expert	-2.62	0.91	-4.94	-1.04	(3)	(3)
Naïve vs SF	-1.51	0.80	-3.44	0.00	(3)	(3)

(1) standardized to its mean
(2) overall effect of the predictor
(3) not shown because of limited interpretation

2.2. Kinematics

Ninety-two out of 96 children operated their apparatus to retrieve the ten eggs contained in the magazine. The four children who did not retrieve eggs were tested in condition ‘Social Facilitation’ and most of them were young (3.8, 4.2, 4.8, and 7.2 years).

2.2.1. Duration until peak

We first assessed whether demonstrators slowed down in the presence of a naïve partner who could copy their actions. The full LMM was not significantly different to the null model from which the predictor condition and its interaction terms were omitted (χ^2 = 17.41, df = 12, N = 1916, p = .135, Table 4.4). Therefore, neither condition nor its interaction with the type of movement, and sex and age of the demonstrator significantly influenced whether children slowed down while operating their apparatus.

Table 4.4 Results of the LMM that assessed whether the variable condition and its interactions with the type of movement and sex and age of the demonstrator influenced the duration until children reached the peak of pulling and turning movements.

Term	Estimate	SE	lower CI	upper CI	χ^2	*P*
Intercept	0.28	0.08	0.11	0.44	(3)	(3)
Condition						
Naïve vs Expert	0.06	0.12	-0.17	0.30	(3)	(3)
Naïve vs SF	0.16	0.13	-0.1	0.42	(3)	(3)
Naïve vs Empty	0.18	0.12	-0.05	0.42		
Sex Dem F vs M	0.02	0.12	-0.21	0.26	(3)	(3)
Age Dem(1)	-0.09	0.06	-0.2	0.03	(3)	(3)
Mov. Type Pull vs Turn	-0.08	0.06	-0.19	0.04	(3)	(3)
Segment Number(1)	-0.12	0.01	-0.15	-0.09	55.37(2)	<.001(2)
Condition*Sex Dem					2.87(2)	.412(2)
Naïve vs Expert	-0.26	0.16	-0.58	0.06	(3)	(3)
Naïve vs SF	-0.08	0.18	-0.42	0.27	(3)	(3)
Naïve vs Empty	-0.05	0.17	-0.38	0.28	(3)	(3)
Condition*Age Dem(1)					4.34(2)	.227(2)
Naïve vs Expert	-0.1	0.08	-0.28	0.04	(3)	(3)
Naïve vs SF	0.05	0.09	-0.13	0.23	(3)	(3)
Naïve vs Empty	0.02	0.08	-0.14	0.18	(3)	(3)
Condition*Mov. Type					4.81	.186
Naïve vs Expert	0.14	0.08	-0.03	0.3	(3)	(3)
Naïve vs SF	0.05	0.09	-0.12	0.23	(3)	(3)
Naïve vs Empty	-0.04	0.08	-0.2	0.13	(3)	(3)

(1) standardized to its mean (Age Dem), transformed as described in section 1.2.1. (Segment Number)
(2) overall effect of the predictor
(3) not shown because of limited interpretation

2.2.2. Separation of movements

We further gauged whether children separated the two movements while operating the own apparatus. Figure 4.9 shows the mean duration between the onset of the pulling and onset of turning movements exhibited by the demonstrators. Demonstrators separated their movements most when no partner was present and least when another trained child was present.

Comparing the full LMM with the respective model from which the main effect of condition and its interaction terms with the age and sex of the demonstrator were absent, yielded a significant result (χ^2 = 17.67, *df* = 9, *N* = 884, *p* = .039). Given that the interaction terms were nonsignificant we omitted them and reran the analysis to be able to assess the main effect of condition. The full-null comparison again yielded a significant result (χ^2 = 14.49, *df* = 3, *N* = 884, *p* = .002; see Table 4.5). Demonstrators separated their movements significantly least in condition 'Expert' and most in condition 'Empty', while there was no difference between condition 'Naïve' and 'Social Facilitation'. This effect was independent of the demonstrators' age or sex.

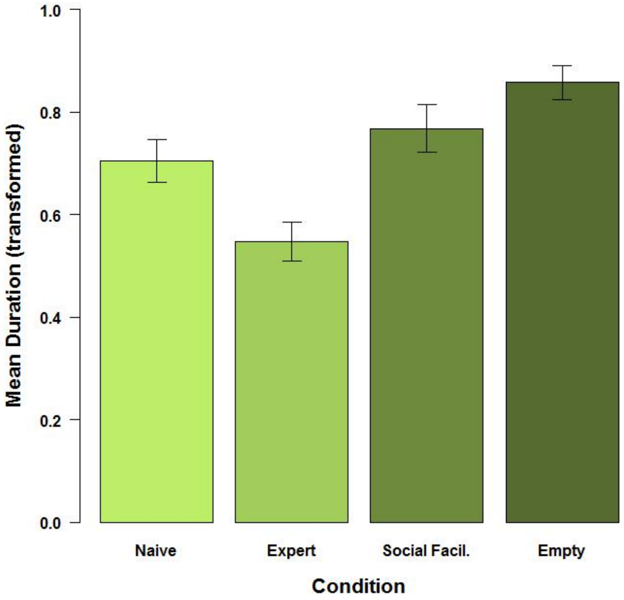

Figure 4.9 Mean duration (its scale was transformed as stated in section C1, 1.2.2.; p. 151) between the onset of the pulling and onset of turning movement in experiment 'Independent'. Smaller values show less separation of both movements. 95% confidence intervals are depicted.

Table 4.5 Results of the LMM that assessed whether the variable condition influenced the duration between the start of the pulling and the start of the turning movement.

Term	Estimate	SE	lower CI	upper CI	χ^2	*P*
Intercept	0.78	0.06	0.66	0.91	(3)	(3)
Condition					14.49(2)	.002(2)
Naïve vs Expert	-0.16	0.08	-0.32	-0.00	(3)	(3)
Naïve vs SF	0.08	0.08	-0.09	0.24	(3)	(3)
Naïve vs Empty	0.13	0.08	-0.02	0.29	(3)	(3)
Sex Dem F vs M	-0.14	0.06	-0.26	-0.03	5.87(2)	.015(2)
Age Dem(1)	-0.12	0.03	-0.18	-0.06	15.8(2)	<.001(2)
Segment Number(1)	-0.14	0.02	-0.18	-0.1	34.2(2)	<.001(2)

(1) standardized to its mean
(2) overall effect of the predictor
(3) not shown because of limited interpretation

2.3. Ontogeny of strategies used

Finally, we investigated whether the communicative strategies used by the demonstrator significantly increased or decreased as a function of the demonstrator's age. Figure 4.10 shows the number of children that exhibited the different communicative types at least once during the given session. Iconic gestures were exhibited most by 5-year-old children and never by 7-year-olds. In general, each behaviour was exhibited most by 5-year-olds.

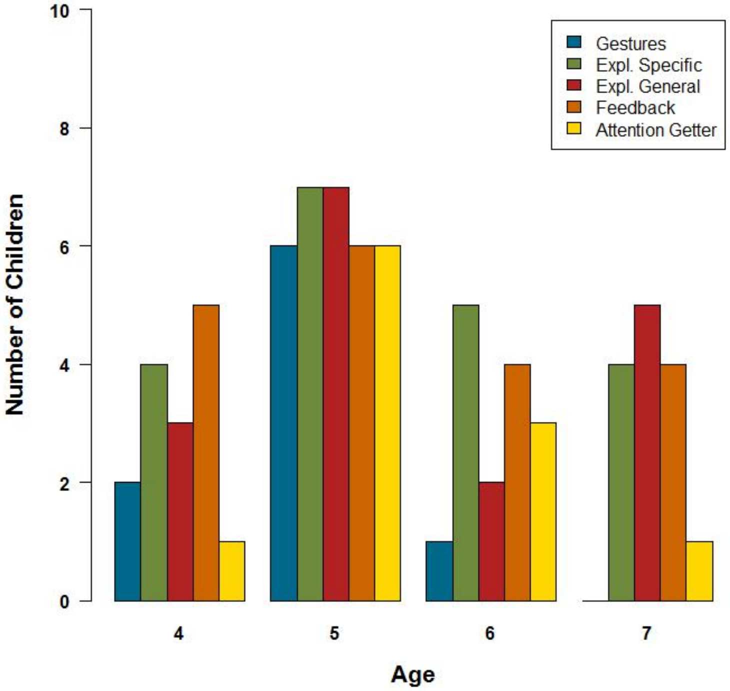

Figure 4.10 Number of children that exhibited the respective communicative type at least once during the given session of experiment 'Independent'. All conditions are included. To facilitate visualizing the data, we treated age as a categorical instead of a continuous variable as in the model. In each age group, we tested a total of 18 children (excluding condition 'Empty').

Nevertheless, the GLMM that included the interaction between communication type and the demonstrator's age did not explain significantly more of the variance in whether communicative instances occurred than a model that did not include this interaction (χ^2 = 3.98, *df* = 4, *N* = 360, *p* = .409; see Table 4.6). Thus, it seems that age did not significantly influence whether some behaviours were exhibited or not.

Table 4.6 Results of the GLMM that assessed whether demonstrators showed a change in their use of communicative strategies depending on their age.

Term	Estimate	SE	lower CI	upper CI	χ^2	*P*
Intercept	0.19	0.75	-1.39	1.70	(3)	(3)
Comm. Type						
Expl.S vs Att.Gett	-1.43	0.6	-2.67	-0.30	(3)	(3)
Expl.S vs Expl.G	-0.42	0.53	-1.48	0.61	(3)	(3)
Expl.S vs Feedback	-0.14	0.52	-1.17	0.88	(3)	(3)
Expl.S vs Iconic	-2.17	0.73	-3.78	-0.86	(3)	(3)
Age Dem(1)	-0.09	0.44	-0.97	0.79	(3)	(3)
Sex Comp.					4.75(2)	.191(2)
FF vs FM	-1.03	0.95	-3.05	0.89	(3)	(3)
FF vs MF	0.51	0.89	-1.28	2.43	(3)	(3)
FF vs MM	0.89	0.86	-0.79	2.78	(3)	(3)
Condition					22.96(2)	<.001(2)
Naïve vs Expert	-3.68	0.87	-5.72	-2.14	(3)	(3)
Naïve vs SF	-2.56	0.78	-4.37	-1.11	(3)	(3)
Comm.Type*Age(1)					3.98(2)	.409(2)
Expl.S vs Att.Gett	-0.19	0.59	-1.38	0.96	(3)	(3)
Expl.S vs Expl.G	0.13	0.52	-0.89	1.17	(3)	(3)
Expl.S vs Feedback	-0.26	0.51	-1.29	0.74	(3)	(3)
Expl.S vs Iconic	-1.18	0.73	-2.77	0.16	(3)	(3)

(1) standardized to its mean
(2) overall effect of the predictor
(3) not shown because of limited interpretation

D. Experiment ‘Dependent’ – Analyses and Results

1. Analyses

As in experiment ‘Independent’, we assessed 1) which strategies the demonstrator used to teach and what factors influenced their communication, 2) whether the demonstrator used the own apparatus to teach and what factors influenced their kinematics, and 3) how the age of the demonstrator influenced the teaching strategies.

1.1. Communication

We analysed the data of experiment ‘Dependent’ in the same way we did in experiment ‘Independent’. The model descriptions are therefore shortened and for a full justification of why variables were included refer to section C1, 1.1. (p. 147).

1.1.1. Difference between communication types

We first assessed how the different communication types (i.e. iconic gestures, explaining specific, explaining general, feedback, and attention getter) differed from one another and whether the demonstrators were sensitive to the fact that their help was needed in the test but not the control conditions. We ran a GLMM with a Poisson error structure and log link function (McCullagh & Nelder, 1989). Given that the model was over-dispersed with a dispersion parameter of 1.44 ($\chi^2 = 367.24$, $df = 255$, $p < .001$), we fitted a GLMM with a negative binomial Poisson model and log link function. We did not include condition ‘Empty’ and from the social conditions excluded children that did not talk at all (including the category ‘Other’; 9 dyads overall). The number of observations was 315 of 63 dyads. Our response variable was the count of communicative instances and we again included the log-transformed number of total communicative bouts as an offset term (McCullagh & Nelder, 1989). As key predictors, we included the type of communication (Iconic gestures, Explaining specific, Explaining general, Feedback, and Attention getter), condition (Naïve, Expert, Social Facilitation), and the interaction between both.

The sex combination within a dyad and the z-transformed variable age of the demonstrator were added to control for their influence. Moreover, we integrated the random intercept (Barr et al., 2013; Forstmeier & Schielzeth, 2011) for dyad identity.

1.1.2. Observers’ behaviour

Again, we assessed whether children proactively communicated with their partner or whether this was driven by the behaviour of the partner. The GLMM had a binomial error structure and a logit link function (McCullagh & Nelder, 1989), and the number of observations was 121 of 72 dyads. Our response was whether any of the measured communicative behaviours (i.e. iconic gestures, explaining specific, explaining general, feedback, and attention getter) was exhibited by the given subject. Our two key predictors were again ‘Questions’ (i.e. all questions or active requests) and ‘Helplessness’ (i.e. all non-directional utterances from which the demonstrator could infer the inability of the partner). To reconstruct how we incorporated these variables into the model, refer to section C1, 1.1.2. (p. 148). Additionally, we included the interaction between ‘Helplessness’ and condition. We used the log-transformed duration of each individual phase to include an offset term into the model.

We added the main effect of condition (Naïve, Expert, SF), and the variables sex composition of each dyad and age of the demonstrator to control for their influence. Age was z-transformed. We included the random intercept but no random slopes components (Barr et al., 2013; Forstmeier & Schielzeth, 2011) for dyad identity.

1.2. Kinematics

We again assessed whether children used their own but now empty apparatus to teach and what factors influenced their kinematics. Given that in experiment ‘Dependent’ the demonstrator faced an empty apparatus, the manipulation rates were much lower than in experiment ‘Independent’, which resulted in not sufficient data to perform the same analyses as in experiment ‘Independent’. We therefore only assessed whether children operated their empty apparatus to a different frequency depending on the condition. This measure was obsolete in experiment ‘Independent’ as the demonstrator manipulated the own apparatus to retrieve eggs herself in every condition.

1.2.1. Frequency of total manipulations

To understand whether demonstrators would operate their empty apparatus more frequently when a naïve individual was present that had access to the apparatus, we fitted a GLMM with a Poisson error structure and log link function (McCullagh & Nelder, 1989). The model had a dispersion parameter of 1.98 ($\chi^2 = 265.16$, $df = 134$, $p < .001$) and was clearly over-dispersed. We therefore fitted a GLMM with a negative binomial Poisson model and log link function. The number of observations was 192 of 96 subjects. Our response consisted of the separate count of pull and turn movements executed by the demonstrator. We included an offset term (Barr et al., 2013; Forstmeier & Schielzeth, 2011) to account for different lengths in session durations and that more manipulations could be executed the longer the session lasted. The total duration of each session was log-transformed in order to add the offset term to the model. As our key predictors we included condition with four levels (Naïve, Expert, SF, Empty) and its interaction with the sex and age of the demonstrator.

The type of movement and the main effects of age and sex of the demonstrator were added as additional fixed effects to control for their influence on whether demonstrators operated the empty apparatus. Age was z-transformed before inclusion. We incorporated the random intercept (Barr et al., 2013; Forstmeier & Schielzeth, 2011) for subject identity but no random slopes components (Barr et al., 2013; Forstmeier & Schielzeth, 2011).

1.2.2. Frequency of complete manipulations

In the previous model, we included all movements that the demonstrator performed on the empty apparatus. Therefore, we also considered incomplete movements that consisted only of one of the two actions. To understand whether more complete movements (i.e. pulls and turns that overlapped) occurred in the test compared to the control conditions we fitted an additional model. This enabled us to gauge whether children might have performed the entire action sequence more often when the naïve partner needed to learn which actions have to be executed in what order. As was stated in section C1, 1.2.2. (p. 150), for a movement to be considered complete the onset of a pull movement had to occur before the peak of a turn movement, or the turn onset had to occur before the pull end. Thus, we only included movements that were executed in the correct order to potentially acquire an egg. We fitted a GLM with a Poisson error structure and log link function (McCullagh & Nelder, 1989). The model was over-dispersed with a dispersion parameter of 2.27 ($\chi^2 = 123.68$, $df = 84$, $p < .001$). Due to the fact that we had too many zeros in the data and a zero-inflated negative binomial model could not account for it, we fitted a binomial GLM with a logit link function. The number of observations was 96 of 96 subjects. Our response was whether at least one complete movement occurred in a session. Again we included an offset term

(McCullagh & Nelder, 1989) accounting for the total duration of each session. As our key predictors we included condition and its interaction with the age and sex of the demonstrator.

We added the main effects of the demonstrator's age and sex to control for their influence. Age was z-transformed. No random intercepts and slopes were incorporated because each subject just contributed one data point.

1.3. Ontogeny of strategies used

Finally, we investigated how the age of the demonstrator influenced which strategy the demonstrator used to share directly useful information. Given that in experiment 'Dependent' but not 'Independent' the apparatus remained empty it is informative to include a measure of whether children manipulated their apparatus or not. Furthermore, given that we did not find that age influenced the communicative strategies used in experiment 'Independent', we did not include each category but only those that transferred information the partner could directly enact. We therefore considered three different modalities: Verbal (i.e. explaining the specific mechanism), gestures (i.e. using iconic gestures to show it), actions (i.e. demonstrating the action on the own apparatus). We fitted a GLMM with a binomial error structure and logit link function (McCullagh & Nelder, 1989). The number of observations was 216 of 72 dyads. We used the interaction between the mode of communication (i.e. verbal, gesture, demonstration) and the age of the demonstrator as our key predictor. The interaction term informs us whether the modality by which children share specific information with their partner changes with increasing or decreasing age. Age was z-transformed before inclusion.

We included the main effects of modality (Verbal, Gesture, Action), the age of the demonstrator, sex combination within a dyad (F-F, F-M, M-F, M-M), and the type of condition (Naïve, Expert, Social Facilitation) to control for their respective influences. We integrated the random intercept but no random slopes components (Barr et al., 2013; Forstmeier & Schielzeth, 2011) for dyad identity.

2. Results

2.1. Communication

2.1.1. Difference between communication types

First, we assessed whether children exhibited the different communication types to a different degree to each other and between conditions. Figure 4.11 shows the mean number of bouts of each communicative type that children exhibited in each of the three social conditions. Across conditions, 44 out of 72 demonstrators communicated with their partners in a relevant manner. As in experiment 'Independent', we did not observe any of the coded behaviours except for 'Other' (see section 2.8.) in the control condition 'Empty'. As in experiment 'Independent', children explained the specific mechanism most. This was followed by iconic gestures, general explanations, feedback, and attention getter.

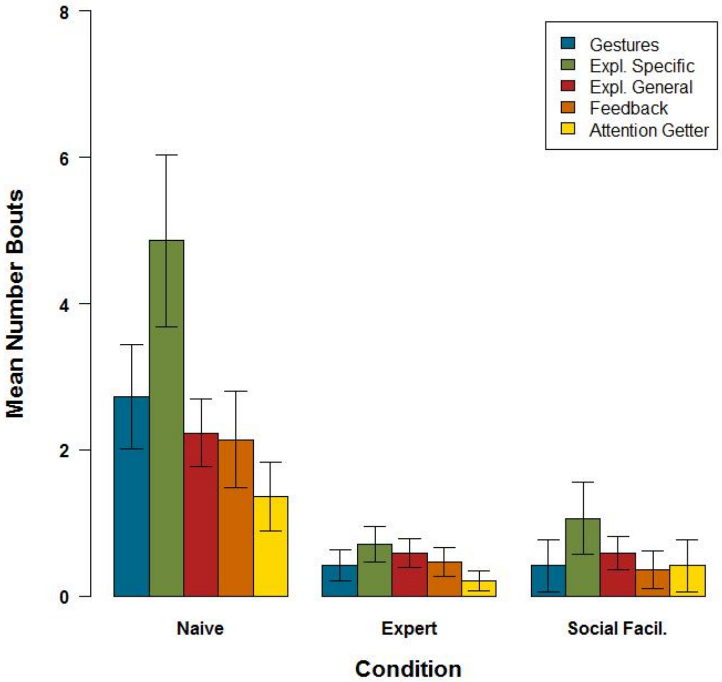

Figure 4.11 Mean number of bouts of each communicative type that children exhibited in each of the three social conditions of experiment 'Dependent' and corresponding 95% confidence intervals.

The GLMM including the type of communication, condition, and the interaction between the two was significant in comparison to the respective null model (χ^2 = 23.53, *df* = 10, *N* = 315, *p* = .009). The interaction between communication type and condition was not significant and (χ^2 = 1.61, *df* = 8, *p* = .991), so we omitted it to assess the main effects. The GLMM including the two predictors condition and communication type was again significant in comparison to the null model (χ^2 = 21.93, *df* = 2, *N* = 315, *p* < .001, Table 4.7).

Condition significantly influenced the amount of observed communicative bouts (χ^2 = 21.93, *df* = 2, *p* < .001). Overall more communication occurred in condition 'Naïve' compared to the two social control conditions (see Figure 4.11). Releveling the categories of the variable condition, so that condition 'Social Facilitation' was the reference group, revealed that the two control conditions were non-significantly different to each other. In comparison to experiment 'Independent' we see a slight increase in communication in condition 'Expert'.

The type of communication was significant (χ^2 = 25.47, *df* = 4, *p* < .001), which means that the frequency in which the five behaviours was exhibited differed to each other. Releveling the categories of the variable communication type showed that none of the other categories was significantly different from each other, except that children overall gave general explanations (Estimate±SE = 0.75±0.28, lowerCI = 0.2, upperCI = 1.31, χ^2 = 2.64, *p* = .008) and iconic gestures (Estimate±SE = 0.62±0.28, lowerCI = 0.07, upperCI = 1.18, χ^2 = 2.18, *p* = .029) more often than they tried to get the attention of their partner.

Table 4.7 Results of the GLMM that assessed whether the number of bouts of each communication type was different between types and between conditions.

Term	Estimate	SE	lower CI	upper CI	χ^2	P
Intercept	-2.03	0.28	-2.60	-1.50	(3)	(3)
Condition					21.93(2)	<.001(2)
Naïve vs Expert	-0.98	0.25	-1.52	-0.50	(3)	(3)
Naïve vs SF	-1.06	0.27	-1.63	-0.55	(3)	(3)
Comm. Type					25.47(2)	<.001(2)
Expl.S vs Att.Gett	-1.25	0.27	-1.78	-0.73	(3)	(3)
Expl.S vs Expl.G	-0.50	0.24	-0.98	-0.02	(3)	(3)
Expl.S vs Feedback	-0.82	0.25	-1.31	-0.33	(3)	(3)
Expl.S vs Iconic	-0.63	0.24	-1.11	-0.15	(3)	(3)
Age Dem(1)	-0.05	0.11	-0.28	0.17	0.21(2)	.649(2)
Sex Comp.					3.96(2)	.266(2)
FF vs FM	0.29	0.31	-0.35	0.93	(3)	(3)
FF vs MF	-0.08	0.30	-0.69	0.53	(3)	(3)
FF vs MM	0.41	0.28	-0.14	1.01	(3)	(3)

(1) standardized to its mean
(2) overall effect of the predictor
(3) not shown because of limited interpretation

2.1.2. Observers' behaviour

Furthermore, we investigated how the behaviour of the observer (i.e. direct and indirect indicators of needing help) influenced whether the demonstrator provided communicative help. Figure 4.12 indicates whether demonstrators communicated proactively or only after the partner expressed his or her inability verbally. It shows that 30 out of 72 demonstrators already started to communicate in a relevant manner without the partner first directly (i.e. 'Questions') or indirectly (i.e. 'Helplessness') expressing his or her inability. Out of these, 14 demonstrators were tested in condition 'Naïve', 9 in condition 'Expert', and 7 in condition 'Social Facilitation'. In comparison to experiment 'Independent', we observed an increase from 2 to 9 demonstrators that communicated proactively in condition 'Expert'. In condition 'Naïve', 14 instead of 13 demonstrators did so, while the number remained the same in condition 'Social Facilitation'.

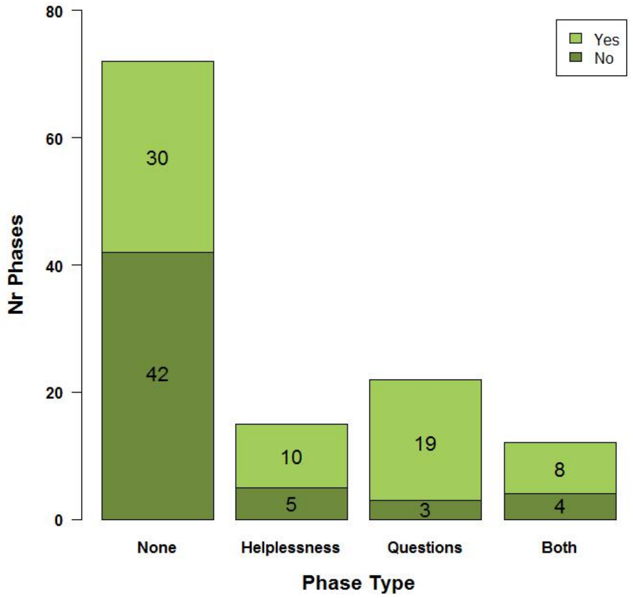

Figure 4.12 Number of different types of phases across all three social conditions in experiment 'Independent', split by phases in which the demonstrator did and did not communicate in a relevant manner. The total number of dyads is the sum of 'None' phases, given that partners never uttered questions or helplessness on second one of a session. In 30 sessions, partners did not exhibit questions and helplessness before the demonstrator communicated in a relevant manner.

The GLMM that investigated the influence of direct (i.e. 'Questions') and indirect (i.e. 'Helplessness') utterances on the likelihood of the demonstrator communicating with the partner yielded a significant result (χ^2 = 12.15, *df* = 4, *N* = 121, *p* = .016). The interaction between conditions and 'Helplessness' was only borderline significant (χ^2 = 5.61, *df* = 2, *p* = .061), so we omitted it from the model to interpret the main effect of 'Helplessness'. The new model comprising the predictors 'Questions' and 'Helplessness' yielded a significant result (χ^2 = 6.54, *df* = 2, *N* = 121, *p* = .038, Table 4.8). 'Helplessness' did not contribute to explaining why demonstrators communicated in a relevant manner. However, questions or active requests by the partner significantly increased the likelihood that the demonstrator responded (χ^2 = 6.44, *df* = 1, *p* = .011). Thus, demonstrators were reactive to questions but not helplessness and responded by communicating with the partner in a relevant manner.

As in experiment 'Independent', partners did not express questions or helplessness first much more frequently than the other: 15 out of 72 partners first uttered helplessness such as "I lost it" or "This is difficult", whereas 22 partners first directly requested help through questions targeted at the demonstrator or making direct statements such as "Please explain". Thus, the model should not be influenced by a greater frequency of one type occurring first.

Table 4.8 Results of the GLMM that assessed whether the behaviour of the partner influenced whether the demonstrator communicated in a relevant manner.

Term	Estimate	SE	lower CI	upper CI	χ^2	*P*
Intercept	1.17	0.69	-0.17	2.73	$^{(3)}$	$^{(3)}$
Questions No vs Yes	1.70	0.72	0.37	3.31	$6.44^{(2)}$	$.011^{(2)}$
Helpless No vs Yes	-0.21	0.64	-1.47	1.13	$0.10^{(2)}$	$.749^{(2)}$
Age Dem$^{(1)}$	0.27	0.27	-0.28	0.84	$1.00^{(2)}$	$.317^{(2)}$
Sex Comp.					$0.31^{(2)}$	$.959^{(2)}$
FF vs FM	0.19	0.8	-1.48	1.87	$^{(3)}$	$^{(3)}$
FF vs MF	0.34	0.79	-1.32	2.03	$^{(3)}$	$^{(3)}$
FF vs MM	0.40	0.78	-1.28	2.00	$^{(3)}$	$^{(3)}$
Condition					$20.78^{(2)}$	$<.001^{(2)}$
Naïve vs Expert	-1.67	0.67	-3.25	-0.38	$^{(3)}$	$^{(3)}$
Naïve vs SF	-3.24	0.74	-5.06	-1.93	$^{(3)}$	$^{(3)}$

$^{(1)}$ standardized to its mean
$^{(2)}$ overall effect of the predictor
$^{(3)}$ not shown because of limited interpretation

2.2. Kinematics

Sixty-two out of 96 children operated their apparatus even though it remained empty throughout the entire experiment.

2.2.1. Frequency of total manipulations

We first assessed whether demonstrators operated their empty apparatus more frequently in the test compared to the control conditions, and how this interacted with the demonstrator's age and sex. Figure 4.13 shows the mean frequency of manipulations during a session in each of the four conditions. Demonstrators of condition 'Expert' operated their empty apparatus least frequently in comparison to the other conditions.

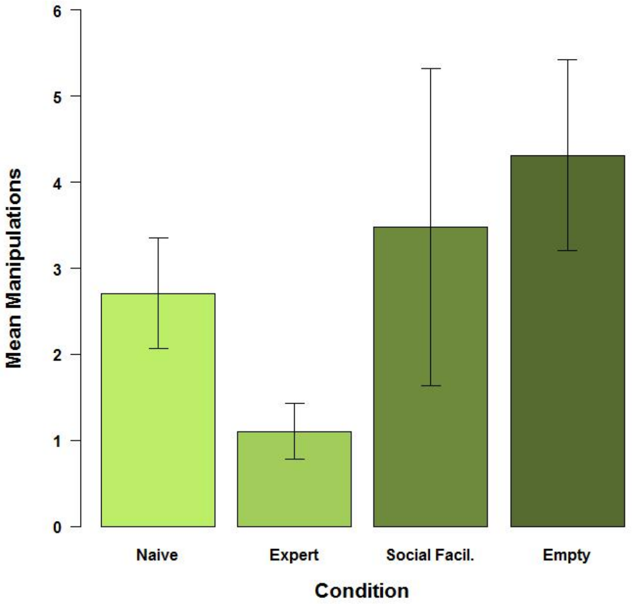

Figure 4.13 Mean frequency of manipulations during a session in each of the four conditions of experiment ‘Dependent’, and corresponding 95% confidence intervals.

The GLMM was significantly different to a model from which condition and its interactions with the sex and age of the demonstrator was omitted ($\chi^2 = 18.03$, *df* = 9, *N* = 192, *p* = .035). Only the interaction between condition and sex of the demonstrator was borderline significant ($\chi^2 = 6.91$, *df* = 3, *p* = .075). We therefore omitted both interactions to be able to assess the main effect of condition. The model was significant in comparison to a model from which condition was omitted ($\chi^2 = 10.40$, *df* = 3, *N* = 192, *p* = .015; see Table 4.9). Children operated their empty apparatus significantly less often in condition ‘Expert’ compared to each of the three other conditions, while there was no significant difference between the other three conditions.

Table 4.9 Results of GLMM that assessed whether the variable condition explained the amount of total manipulations exhibited in experiment 'Dependent'.

Term	Estimate	SE	lower CI	upper CI	χ^2	P
Intercept	-5.76	0.41	-6.75	-5.15	(3)	(3)
Condition					10.41(2)	.015(2)
Naïve vs Expert	-0.97	0.52	-2.03	0.09	(3)	(3)
Naïve vs SF	-0.63	0.50	-1.59	0.38	(3)	(3)
Naïve vs Empty	0.53	0.47	-0.41	1.49	(3)	(3)
Sex Dem F vs M	0.82	0.36	0.16	1.53	5.20(2)	.023(2)
Age Dem(1)	0.24	0.18	-0.12	0.6	1.78(2)	.182(2)
Mov. Type Pull vs Turn	0.75	0.19	0.35	1.08	15.90(2)	<.001(2)

(1) standardized to its mean
(2) overall effect of the predictor
(3) not shown because of limited interpretation

2.2.2. Frequency of complete manipulations

Further, we investigated whether more complete movements occurred in the test than the control conditions, which would show that demonstrators used coherent movements in the presence of a naïve individual that could deliver eggs to the demonstrator. Figure 4.14 shows that the mean frequency of complete manipulations was very low in each condition, and close to zero in condition 'Expert'. The full-null comparison was non-significant (χ^2 = 11.09, *df* = 9, *N* = 96, *p* = .27; see Table 4.10), so condition and its interactions with the age and sex of the demonstrator did not significantly contribute to explaining the amount of complete movements that occurred. Given that close to zero complete manipulations were exhibited by children in condition 'Expert', the standard errors for the associated comparisons between condition 'Naïve' and 'Expert' are very large and respective statistics have to be interpreted with caution.

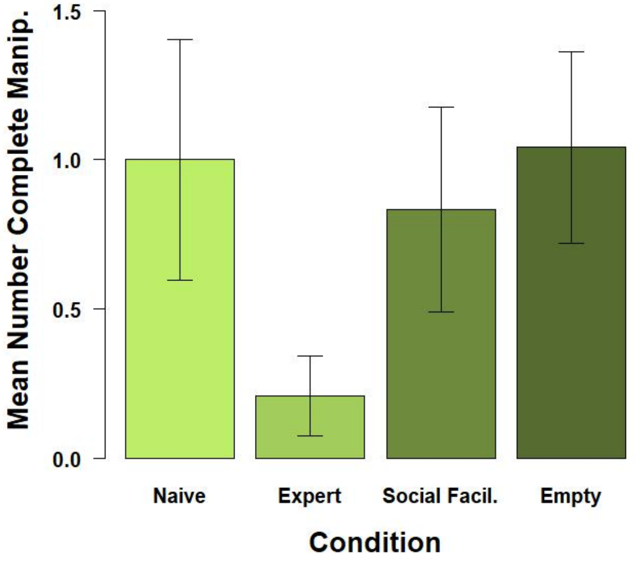

Figure 4.14 Mean number of complete manipulations within a session of experiment 'Dependent' for each of the four conditions.

Table 4.10 Results of GLM that assessed whether the variable condition and its interaction with the age and sex of the demonstrator influenced the amount of complete movements exhibited in experiment 'Dependent'.

Term	Estimate	SE	lower CI	upper CI	χ^2	*P*
Intercept	-5.77	0.62	-7.05	-4.55	(3)	(3)
Condition						
Naïve vs Expert	-16.7	1164.74	-16.8	119.91	(3)	(3)
Naïve vs SF	-1.25	1.05	-3.57	0.71	(3)	(3)
Naïve vs Empty	0.15	0.87	-1.58	1.90	(3)	(3)
Sex Dem F vs M	-0.01	0.88	-1.77	1.75	(3)	(3)
Age Dem(1)	0.26	0.48	-0.70	1.23	(3)	(3)
Condition*Sex Dem					3.54(2)	.315(2)
Naïve vs Expert	16.3	1164.74	-45.46	228.10	(3)	(3)
Naïve vs SF	1.70	1.36	-0.89	4.54	(3)	(3)
Naïve vs Empty	0.80	1.24	-1.62	3.28	(3)	(3)
Condition*Age Dem(1)					0.94(2)	.817(2)
Naïve vs Expert	-0.26	0.86	-2.01	1.48	(3)	(3)
Naïve vs SF	0.42	0.67	-0.86	1.79	(3)	(3)
Naïve vs Empty	0.35	0.67	-0.95	1.72	(3)	(3)

(1) standardized to its mean
(2) overall effect of the predictor
(3) not shown because of limited interpretation

2.3. Ontogeny of strategies used

Finally, we investigated whether the strategies used by the demonstrator significantly changed depending on the demonstrator's age. Figure 4.15 depicts the number of children that exhibited the different teaching strategies at least once during the given session. In contrast to experiment 'Independent', iconic gestures were also exhibited by 7-year-olds. Additionally, we found an increase of both iconic gestures and specific explanations for each age category in comparison to experiment 'Independent'. Finally, in contrast to experiment 'Independent', 5-year-olds did not show the the highest frequency in all categories.

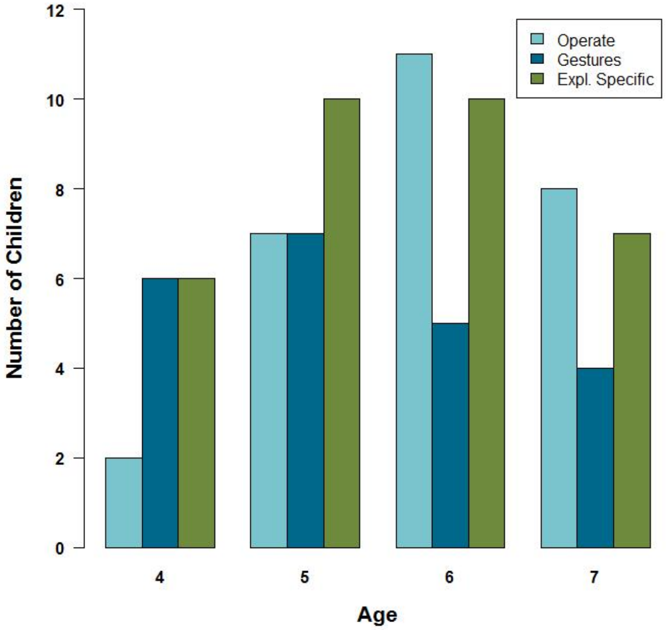

Figure 4.15 Number of children that exhibited the respective behaviour at least once during the given session of experiment 'Dependent'. All conditions are included. For illustrative purposes, we used age as binned categories instead of a continuous variable as in the model. In each age group, we tested a total of 18 children (excluding condition 'Empty').

The GLMM that included the interaction between the teaching strategy and the demonstrator's age was only borderline significant in explaining the variance in whether communicative instances occurred compared to a model that did not include this interaction (χ^2 = 5.74, df = 2, N = 216, p = .057; see Table 4.11). Therefore, we replicated the finding of experiment 'Independent' and did not find an effect of age on the strategies that the demonstrators employed.

Table 4.11 Results of the GLMM that assessed whether demonstrators showed a change in their use of strategies (i.e. verbal, gesture, action) depending on their age.

Term	Estimate	SE	lower CI	upper CI	χ^2	*P*
Intercept	0.31	0.48	-0.66	1.29	(3)	(3)
Strategy						
Operate vs Iconic	-0.42	0.41	-1.24	0.37	(3)	(3)
Operate vs Expl.S	0.42	0.39	-0.34	1.21	(3)	(3)
Age Dem(1)	0.64	0.30	0.06	1.27	(3)	(3)
Sex Comp.					10.43(2)	.015(2)
FF vs FM	-0.62	0.53	-1.73	0.43	(3)	(3)
FF vs MF	0.62	0.5	-0.37	1.66	(3)	(3)
FF vs MM	0.87	0.50	-0.11	1.94	(3)	(3)
Condition					22.73(2)	<.001(2)
Naïve vs Expert	-1.45	0.43	-2.40	-0.64	(3)	(3)
Naïve vs SF	-2.02	0.47	-3.06	-1.16	(3)	(3)
Strategy*Age Dem(1)					5.74(2)	.057(2)
Expl.S vs Iconic	-0.99	0.43	-1.88	-0.17	(3)	(3)
Expl.S vs Operate	-0.58	0.40	-1.39	0.19	(3)	(3)

(1) standardized to its mean
(2) overall effect of the predictor
(3) not shown because of limited interpretation

E. Comparison experiment of ‘Independent’ and ‘Dependent’ – Analyses and Results

1. Analyses

Finally, we compared the two experiments to understand 1) whether children were more inclined to help when they benefitted from it and 2) whether motivational factors influenced the communicative strategies used by the demonstrator. For both models, we only included the three social conditions, as no demonstrator communicated in a relevant manner in condition ‘Empty’. Additionally, we excluded children that did not talk at all in the social conditions (26 dyads overall).

1.1. Frequency of children helping

We assessed whether children were more inclined to provide communicative help when they benefitted from it than when they did not. We fitted a GLM with a binomial error structure and logit link function (McCullagh & Nelder, 1989). The number of observations was 118 of 118 dyads. Our response variable indicated whether the demonstrator exhibited any of the communicative instances, except 'Other' (Yes, No). As key predictors, we included the experiment type ('Independent', 'Dependent') and its interactions with the type of condition (Naïve, Expert, Social Facilitation) and with the age of the demonstrator. The interaction between experiment and condition reveals whether motivational factors influenced the demonstrator differently in some conditions between the two experiments. Thus, children might have been more motivated to help in the test condition of experiment 'Dependent' compared to experiment 'Independent', but the effect might have been different for the other conditions. Similarly, the latter interaction reveals whether with increasing or decreasing age motivational factors affected the demonstrators' inclination to help differently.

We added the main effect of condition and the z-transformed variable age of the demonstrator to control for their sole influence. Moreover, we included the sex combination within a dyad to control for its influence. We did not integrate random intercepts (Barr et al., 2013; Forstmeier & Schielzeth, 2011) as we only had one data point per subject.

1.2. Differences between communication types

Furthermore, we investigated whether the communicative strategies used by the demonstrators changed depending on whether they benefitted or not. We fitted a GLMM with a Poisson error structure and log link function (McCullagh & Nelder, 1989). The model was over-dispersed with a dispersion parameter of 1.17 (χ^2 = 673.56, *df* = 575, *p* = .003), so we fitted a negative binomial Poisson model with a log link function. The number of observations was 590 of 118 dyads. Our response variable was the sum of all communicative instances, except 'Other', that the demonstrator exhibited. We included the log-transformed number of total communicative bouts, including 'Other', as an offset term to account for the differences in how communicative individual children were in general (McCullagh &

Nelder, 1989). We included the interaction between the type of experiment (Independent, Dependent) and type of communication (Iconic gestures, Explaining specific, Explaining general, Feedback, and Attention getter) as the only key predictor.

The main effects of experiment and communication type, condition (Naïve, Expert, SF), and the sex and age of the demonstrator were added to control for their sole influence. Age was z-transformed. Moreover, we integrated the random intercept (Barr et al., 2013; Forstmeier & Schielzeth, 2011) for dyad identity but no random slopes.

2. Results

2.1. Frequency of children helping

Across conditions, children provided more help during experiment 'Dependent' (61.1%) in comparison to 'Independent (45.8%). Figure 4.16 shows the number of children that exhibited any of the relevant communicative types at least once during the session. The difference between the two experiments was due to an increase in the amount of children that provided help in condition 'Naïve' and 'Expert', while the number remained the same in condition 'Social Facilitation'. Thus, in experiment 'Dependent' we observed an increase in how many children provided help when they could actually acquire eggs from their partner. There was an increase in helping in each age group from experiment 'Independent' to 'Dependent' (Figure 4.17).

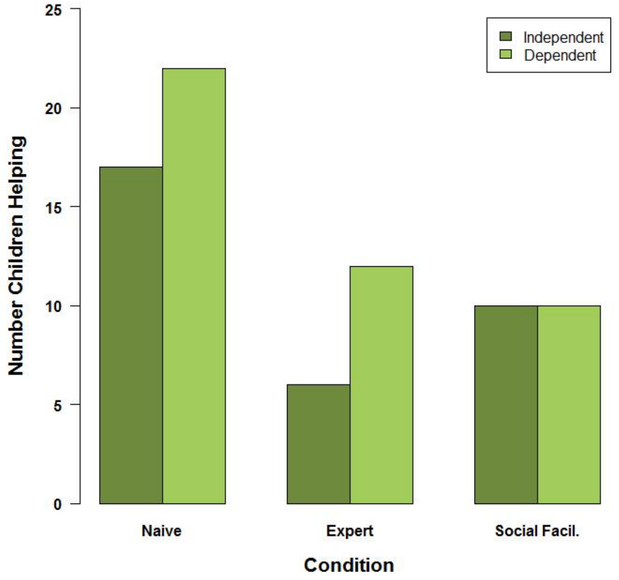

Figure 4.16 Number of children that exhibited any of the relevant communicative types at least once during the given session in each of the three social conditions and in comparison between experiment 'Dependent' and 'Independent'. We tested 24 children in each condition of each experiment.

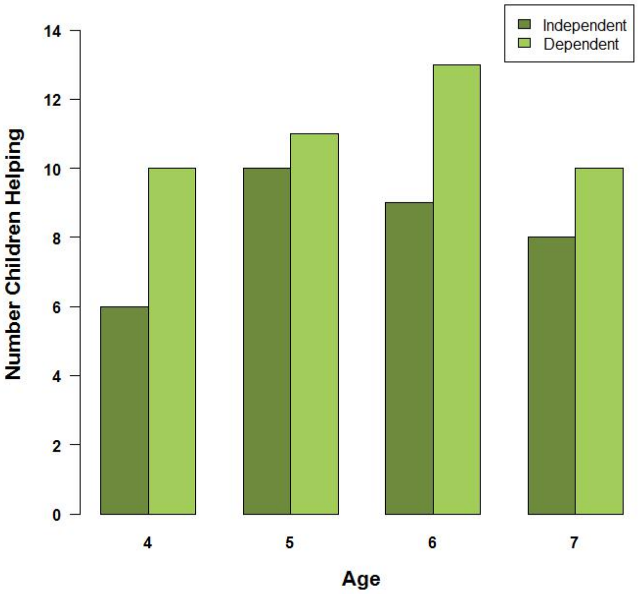

Figure 4.17 Number of children that exhibited any relevant communication at least once in experiment 'Dependent' and 'Independent'. For illustrative purposes, we used age as binned categories instead of a continuous variable as in the model. In each age group, we tested a total of 18 children (excluding condition 'Empty').

Nevertheless, the GLM that included the predictor experiment and its interactions with the condition and the age of the demonstrator was only borderline significant in explaining whether children provided help (χ^2 = 8.21, df = 4, N = 118, p

= .084; see Table 4.12). Thus, children did not provide more help in any of the conditions depending on whether demonstrators benefitted from teaching. Nor did younger or older children provide more help depending on whether they benefitted from it.

Table 4.12 Results of GLM that assessed whether the variable experiment and its interaction with the condition type and the age of the demonstrator influenced the inclination that children provided communicative help.

Term	Estimate	SE	lower CI	upper CI	χ^2	P
Intercept	15.26	15.44	-37.80	65.89	(3)	(3)
Experiment Indep. vs Dep.	-16.08	15.44	-36.92	42.42	(3)	(3)
Condition						
Naïve vs Expert	-17.69	15.44	-29.55	42.45	(3)	(3)
Naïve vs SF	-17.42	15.44	-26.06	43.30	(3)	(3)
Age Dem(1)	-0.24	0.36	-0.96	0.47	(3)	(3)
Sex Comp.					0.62(2)	.892(2)
FF vs FM	0.19	0.72	-1.24	1.60	(3)	(3)
FF vs MF	0.55	0.73	-0.85	2.01	(3)	(3)
FF vs MM	0.35	0.69	-0.99	1.73	(3)	(3)
Condition*Experiment					4.1(2)	.129(2)
Naïve vs Expert	16.13	15.44	-39.58	52.26	(3)	(3)
Naïve vs SF	16.88	15.44	-43.85	25.51	(3)	(3)
Age Dem*Experiment(1)	0.96	0.5	-0.00	1.95	3.83(2)	.050(2)

(1) standardized to its mean
(2) overall effect of the predictor
(3) not shown because of limited interpretation

2.2. Differences between communication types

We further investigated whether children changed their teaching strategies depending on whether they benefitted from it or not. Figure 4.18 shows the mean number of bouts of each communicative type. We observed an increase in each type when children benefitted from the knowledge of their partner in experiment 'Dependent'. The difference was more pronounced for some types, such as iconic gestures.

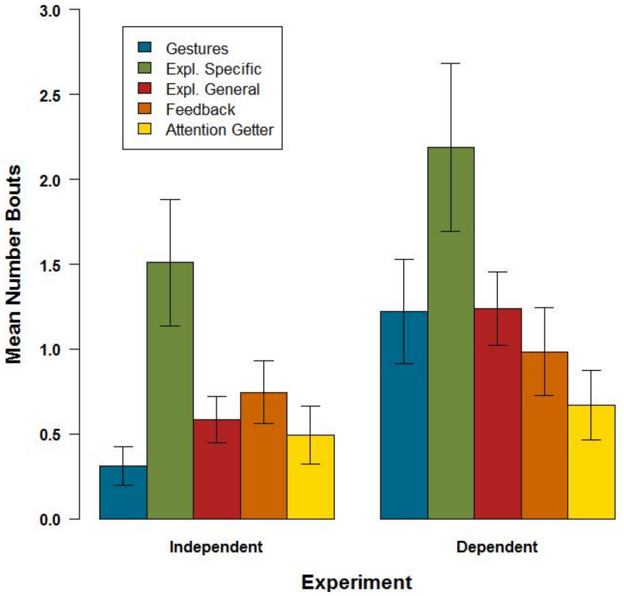

Figure 4.18 Mean number of bouts of each communicative type that children exhibited in experiment 'Independent' and 'Dependent', and corresponding 95% confidence intervals.

The GLMM that included the interaction between the type of experiment and type of communication was significant ($\chi^2 = 9.62$, $df = 4$, $N = 590$, $p = .047$; see Table 4.13). Demonstrators exhibited iconic gestures, specific explanations, and general explanations significantly more frequently when they benefitted from the knowledge of their partner. We did not observe a significant difference between the two experiments regarding the frequency that demonstrators gave feedback and tried to get the attention of their partner.

Table 4.13 Results of GLM that assessed whether the experiment type and its interaction with condition and the age of the demonstrator influenced the inclination that children provided communicative help.

Term	Estimate	SE	lower CI	upper CI	χ^2	*P*
Intercept	-1.91	0.20	-2.32	-1.52	(3)	(3)
Experiment Indep. vs Dep.	0.2	0.26	-0.31	0.71	(3)	(3)
Comm. Type						
Expl.S vs Att.Gett	-1.21	0.27	-1.73	-0.70	(3)	(3)
Expl.S vs Expl.G	-0.4	0.23	-0.86	0.06	(3)	(3)
Expl.S vs Feedback	-0.81	0.25	-1.29	-0.33	(3)	(3)
Expl.S vs Iconic	-0.59	-0.54	-1.05	-0.13	(3)	(3)
Condition					40.03(2)	<.001(2)
Naïve vs Expert	-1.17	0.20	-1.6	-0.79	(3)	(3)
Naïve vs SF	-0.94	0.19	-1.33	-0.56	(3)	(3)
Age Dem(1)	-0.04	0.08	-0.20	0.13	0.21(2)	.651(2)
Sex Dem. F vs M	0.07	0.16	-0.24	0.39	0.17(2)	.677(2)
Comm.Type*Experiment					9.67(2)	.046(2)
Expl.S vs Att.Gett	0.05	0.42	-0.76	0.84	(3)	(3)
Expl.S vs Expl.G	-0.40	0.38	-1.16	0.35	(3)	(3)
Expl.S vs Feedback	0.09	0.39	-0.65	0.83	(3)	(3)
Expl.S vs Iconic	-1.09	0.44	-1.94	-0.27	(3)	(3)

(1) standardized to its mean
(2) overall effect of the predictor
(3) not shown because of limited interpretation

F. Discussion

Around 71% of children taught their naïve partner even though they did not directly benefit from it in experiment 'Independent'. They communicated in a relevant manner most when their partner was naïve and could actually make direct use of the information, and never when a partner was absent. Specific explanations were used the most, followed by feedback, general explanations, attention getter, and iconic gestures. Around 76% of the helpful demonstrators of condition 'Naïve' taught their partner proactively, thus, before the partner requested help or was audibly unable to solve the task alone. However, across conditions children did not respond with increased help when their partner asked them to or was audibly struggling. We did not find evidence that demonstrators modified their own motions to facilitate visibility (i.e. slowing down or separating the two actions) for their naïve partner. We also did not find evidence for a change in strategies due to ontogenetic development; already 4-year-olds used a variety of strategies.

In experiment 'Dependent', around 92% of children taught their naïve partner. Again, they used more relevant verbal and gestural communication when there was a need for it in the test condition compared to the control conditions. We replicated the finding that overall children used specific explanations the most. This was followed by iconic gestures (previously used the least), general explanations, feedback, and attention getter. A similar amount of demonstrators of condition 'Naïve' taught their partner proactively (64% of helpful demonstrators, given the increased total number). Children were reactive when their partners asked questions but not when they were audibly struggling. We did not find evidence that children used their empty apparatus to demonstrate the correct motions. We also did not find evidence for a change in strategies due to ontogenetic development.

Comparing the two experiments showed that children did not significantly provide more help when they benefitted from teaching than when they did not, though we observed a numerical increase in children that engaged in teaching when they could actually acquire eggs from their partner (i.e. in the test and expert control condition). The age of the demonstrator did not influence why more children helped in experiment 'Dependent'. Children showed a significant increase in communicative strategies that directly revealed how the mechanism (i.e. specific explanation and iconic gestures) or task (i.e. general explanations) works when they benefitted from their partner's correct actions.

Even without benefitting from teaching, children showed high numbers of relevant communication. Moreover, in both experiments we found a similar number of children who started to communicate proactively before the partner requested help or was audibly unable to solve the task alone. This is in line with previous research on altruism and supports the notion that children are willing to help out of other-regarding preferences. In our experiment, this is extended to teaching and seems to be true for all tested age groups. We found an increase in the number of children that proactively communicated in the expert control condition of experiment 'Dependent' compared to 'Independent'. Thus, in this condition children communicated proactively more often when they benefitted from the actions of their partner. Additionally, across conditions children were more reactive to their partner when they benefitted from their actions, and started to communicate upon being directly requested to do so. Therefore, even though children were motivated to help ignorant partners independent of whether they gained a benefit, they were mostly only motivated to help knowledgeable partners when they obtained rewards through their actions. Two explanations might account for the observed difference in treating partners. In experiment 'Dependent', demonstrators might have started to teach immediately before realizing that their partner already knows how to operate the apparatus. Alternatively, demonstrators might have observed the partners' motions more closely and correct faster given that "their" eggs were at stake as well. This would also explain the increased responsiveness to questions asked (or direct requests made) by the partner. Surprisingly, demonstrators did not significantly react to audible signs that the partner struggled. It might be that these cues were too subtle for them to interpret as worthy to intervene.

Children engaged in teaching when there was a need for it and not just because a partner was present. They never communicated in a relevant manner without an audience, while some children still exhibited verbalizations that we coded as 'Other'. Thus, we are confident that the observed behaviours were teaching episodes in response to a naive partner who was in need of help, and not because of the presence of any audience or because it was self-directed speech that might support some other non-social function. The only exception to this, demonstrators of the social facilitation control condition of experiment 'Independent' explained the specific mechanism to a statistically similar frequency as in the test condition. In experiment 'Dependent', they used specific explanations to a comparable degree in the social facilitation control condition. However, since there was a substantial increase of specific explanations in the test condition of experiment 'Dependent', the two frequencies now were significantly different to one another. Furthermore, in experiment 'Independent' but not 'Dependent', we found a difference between the two social control conditions: While children rarely communicated when the partner was trained in experiment 'Independent', they did so to a similar degree as in the social facilitation control condition in experiment 'Dependent'. Thus, we found an increase in relevant communication only when the partner could make use of the information (i.e. test and expert control condition), while it remained the same when the naïve partner could not make direct use of the information (i.e. social facilitation control condition). Given that the frequency remained the same in the social facilitation control condition independent of whether the demonstrator benefitted from communicating, we suggest that any relevant communication we observed in this condition could reveal a baseline level of sharing knowledge for the sake of sharing it instead of teaching. During coding, we observed that demonstrators in the social facilitation control often but not always talked in past tense (i.e. that the task was to pull and turn), while in the test condition they talked in present tense (i.e. that the task is to pull and turn). Given that we did not anticipate this difference, we adhered to our coding scheme and counted both as explaining the specific mechanism. However, future studies could account for this difference and adjust their coding scheme to further reveal the possible difference between intentional teaching and talking about experiences.

We further analysed how the motivation underlying teaching influenced the communicative strategies used and found that in both experiments children used specific explanations the most. Interestingly, iconic gestures were exhibited to a much greater extent and was the second most frequently used strategy in experiment ‘Dependent’, while it was the least frequently used strategy in experiment ‘Independent’. One explanation could have been that children were operating their own apparatus in the latter experiment and, hence, their hands were occupied. Nevertheless, in most cases children stopped operating their own apparatus during communicative episodes and thus could have also used gestures as well. This difference can therefore not be fully explained by an occupation of the hands and might point towards a different motivation that influenced the usage of iconic gestures. Furthermore, specific and general explanations were exhibited to a greater degree when children benefitted from teaching. Only feedback and attention getter were exhibited to a comparable degree between the two experiments. Therefore, children showed an increase in communicative strategies that directly revealed how the mechanism (i.e. specific explanation and iconic gestures) or task (i.e. general explanations) works when they benefitted from their partner correctly operating the apparatus.

We used a Polhemus motion tracker to record the exact movements that children performed on their respective apparatuses. The analyses showed that contrary to our assumption, children did not slow down while retrieving eggs themselves in experiment 'Independent'. Children did however separate the movements in some conditions more than others. They separated their movements least in the expert control and most in the empty control condition, while there was no difference between the test and social facilitation control condition. This finding is similar to what we found the chimpanzees to be doing. Even though chimpanzees did not separate their movements more in one of the conditions, they were exhibiting pulling movements fastest in the expert control condition and slowest in the empty control condition. Given that speed can affect both the overall velocity and the separation between movements, it seems that children and chimpanzees acted slowest when no partner was present and fastest when another trained individual simultaneously executed the same actions. Thus, either competition or response facilitation might have influenced the behaviour of children as well. We actually observed a lot of children in the expert control condition who counted out loud each additional egg they retrieved and sometimes also explicitly stated that they are better or faster. The fact that children performed the exact same task next to one another therefore often seemingly resulted in a race between the two partners. We did not find a difference between the test and social facilitation control condition, so children seemed to react the same way when facing a naïve partner that needed information and a naïve partner that did not. Given that demonstrators also started to explain the specific mechanism in this condition to a similar degree as in the test condition, one explanation could be that the degree in which they separated their actions reflected their inclination to transmit knowledge as well. Nevertheless, we would need an additional control condition to support this claim and cannot conclude from the data we have that children actively modified their behaviour to teach. A relevant control condition that could be used to distinguish between the two explanations might be a naïve child sitting next to the demonstrator as in the social facilitation condition but who, in contrast to this condition, cannot hear the demonstrator and is turned away from him or her. As for the chimpanzees, we therefore do not have evidence that children modified their own actions on a regular basis to demonstrate the movements while operating the own apparatus in experiment 'Independent'. Still, while coding we did observe instances in which children explicitly asked the other child to watch them and subsequently performed the correct actions on the own apparatus. It seems however that these instances might have either been too rare or executed at the same speed as each of the other actions.

In experiment 'Dependent', 65% of children operated their apparatus at least once even though it remained empty throughout the entire experiment. There was no difference between conditions in the frequency of complete movements (i.e. co-occurring pull and turn movements) that could have been used to demonstrate the entire action sequence. Children did, however, manipulate their empty apparatus to a different frequency between conditions. They operated their empty apparatus least often in the expert control condition, while there was no difference between each of the three other conditions. The most parsimonious explanation for this difference is that children were occupied with gathering eggs and hence manipulated the own apparatus less often. Therefore, as in experiment 'Independent' we did not find evidence that children used their own apparatus to transmit knowledge to their partner. One reason that children of both experiments did not use their apparatus to demonstrate the actions on a regular basis might be that it was less effortful to verbalize or use gestures in order to convey how the task worked. Moreover, observers might have benefitted from verbal instructions as they could execute the instructions at the same time and without having to look at the demonstrator, which is more efficient and places less cognitive load on the observer. Nevertheless, we expected that using an apparatus would grant young demonstrators the advantage to compensate for possible difficulties in successfully explaining how the task works.

To understand whether young demonstrators indeed used different strategies, we assessed how the frequency of observed teaching strategies changed with increasing age. Contrary to previous research, we did not find evidence for a change in strategies due to ontogenetic development. Given that children had to operate their own apparatus in experiment 'Independent', we did not include the strategy of demonstrating the movements on the own apparatus. Even though we found that in experiment 'Independent' all communicative behaviours were exhibited more by 5-year-olds than by any other age group, we did not find statistical support for this. Moreover, iconic gestures were exhibited most by 5-year-old children, rarely by 4- and 6-year-olds, and never by 7-year-olds. In experiment 'Dependent', the apparatus remained empty and we included operating it as an additional strategy. Instead of including all five communicative strategies we only included strategies that directly conveyed information to which actions needed to be performed in order to retrieve eggs. We again did not find evidence for a change in strategies due to ontogenetic development. In contrast to experiment 'Independent', iconic gestures were exhibited by 7-year-olds as well and to a greater degree by all other age groups. Moreover, 6- and 7-year-olds now performed more similar to 5-year-olds than in experiment 'Independent'. One reason of why we did not find an age difference in terms of teaching strategies used, might be that the rate of children that failed during the training phases was increasing with decreasing age (45.5% of 4-year-olds that we tried to train did not pass). Thus, young children that did succeed in training might not be as representative of the entire spectrum of 4-year-olds. Nevertheless, a sufficient amount of 4-year-olds did pass training and were adept at using varied teaching strategies.

This study provided a unique opportunity to study both how teaching strategies of young children were influenced by their motivation, and which strategies they used depending on their age. To summarize, children engaged in teaching proactively and with altruistic intentions. They predominantly taught when there was a need for it and not just because a partner was present. While the number of children that engaged in teaching was not significantly different when they benefitted from their help than when they did not, the strategies that they used changed. Specific explanations remained the most frequently used strategy, however, when children benefitted from teaching they used substantially more iconic gestures and also explained the motions and task more frequently. Thus, they ensured that the information was transmitted via different modalities, and represented what the partner needs to do through verbal and gestural means. They additionally provided more content about the task and its rules. Children used feedback and attention getters to a similar degree irrespective of whether they benefitted from their help. Contrary to our expectation, children of all age groups did not use their apparatus to demonstrate the correct actions. Given that we did not find a change in communicative strategies used depending on the age of our subjects, 4-year-olds already seemed to make use of different strategies and might not have needed to rely on demonstrating the actions with their apparatus. This is new with respect to previous research that suggested that young children predominantly use demonstrations instead of verbal explanations. In contrast, we show that young children were already quite sophisticated in terms of teaching. Unfortunately, children younger than 3.5 did not pass the training, so future research could adapt the task slightly to investigate whether they would then demonstrate the actions and how children change their own motions in order to teach.

We used a similar design to study teaching in chimpanzees (refer to Chapter 3) and in children. The results overlap in that neither species used their own apparatus to a significant degree to demonstrate the motions. However, children but not chimpanzees used gestures to show which motions needed to be performed. Yet, the frequency of gestures only made up a portion of children's communicative repertoire and in addition they used verbal communication to a great extent. Verbal communication granted the advantage that the partner could execute the motions at the same time that the trained subject was instructing. Similarly, the subject could verbalize what needed to be done simultaneous to performing the motions on her apparatus. Thus, she could use two sources of information at the same time, which might have benefitted the partner and, at least in experiment 'Independent', allowed the subject to simultaneously retrieve eggs herself and minimize costs of teaching. We decided to allow the use of verbal communication as we wanted to understand the natural occurrence of teaching in children and which means they predominantly use. We are aware that this diminishes a clear comparison between the two studies, however, enables us to understand the natural repertoire of communication that each species makes use of. To understand whether children start to use physical means to demonstrate actions, future studies could include two conditions that differ in whether children are allowed to talk or not. This would help to understand the degree of flexibility that children possess depending on their age, and would further support a reconstruction of the ontogenetic development of teaching abilities.

Additionally, future studies could include measures of non-verbal communication such as gaze-alternation, pointing, smiling, and gesturing while speaking (i.e. using abstract deictic gestures). The first two signals could function as ostensive cues and facilitate learning in the partner, while the third might function as motivation or positive feedback. The latter signal would give a measure of how complex the task is for a given child. According to the information packaging hypothesis, humans use representational gestures while speaking when the mental content they want to convey through language is difficult for them to structure and verbalize (Kita, 2000). Therefore, measuring the occurrence of such gestures would enable a fine tuned assessment of whether younger children have more difficulty during specific verbal episodes even though they already make use of these. Furthermore, cross-cultural studies would help to understand to what extend our results are generalizable. We do not yet know whether verbal communication during teaching instances is universal in humans or only found in some cultures. Moreover, the style of verbal communication might differ between cultures with some relying more on e.g. direct explanations or feedback than others. Cross-cultural studies will be essential to address theories that teaching and language are tightly interlinked and are an essential part of how human technology evolved.

V. Chapter 5: Conclusions & General Discussion

In this dissertation, I discussed three studies that assessed 1) the ability and motivation of bonobos and chimpanzees to instrumentally help a conspecific, 2) chimpanzees' ability and motivation to teach a conspecific, and 3) children's ability and motivation to teach a conspecific and the ontogenetic development of their teaching strategies. Our main findings were that 1) bonobos but not chimpanzees are motivated to help a conspecific without gaining a direct benefit and help at a constant level when self-interests are induced. Bonobos might have been more susceptible to begging in the helping task, which might have led to an enhanced understanding of the task and subsequently resulted in a better performance in the cooperation task. Furthermore, 2) we did not find evidence that chimpanzees teach a learned action sequence to their conspecifics even when they would have benefitted from the conspecific performing the correct actions. We could, however, show that the new method of using motion trackers worked. Finally, 3) children were willing to engage in teaching independent of whether they gained a direct benefit from it or not. Nevertheless, the teaching strategies changed depending on whether they benefitted from their partner's actions, in that children used more specific and general explanations and more iconic gestures when they acquired rewards through their partner's correct actions. In our study and contrary to previous research, 4-year-olds showed varied teaching strategies and relied more on verbal communication than on physical demonstrations.

I will first review the findings of each study in more depth and subsequently draw the results of each study together and discuss them in light of what factors seem to be necessary to express cumulative culture.

A. Do chimpanzees and bonobos act altruistically and cooperatively towards a conspecific?

Female bonobos shared tools with female partners even when they did not benefit from it. Once they did benefit from it, they shared tools on a consistent level.

Reaching by the partner influenced the likelihood that tools were shared in both experiments. Even though chimpanzee partners reached to a statistically similar degree, chimpanzee helpers did not transfer tools even when they could have benefitted from it. As was discussed earlier, there might be different explanations for a lack of tool transfers by chimpanzee helpers in the helping and cooperative task.

Our experiment 'Helping' was very similar to the study by Yamamoto and colleagues (2009, 2012) with the main difference that chimpanzees were not able to stick their entire arm through the mesh but only their fingers, and that they could complete their own task and retrieve food themselves. Both factors (i.e. either a lack of strong harassment or a lack of boredom) suggest that altruistic responses of chimpanzees might not be due to other-regarding preferences. We showed that once these factors are reduced, chimpanzees were not willing to help their conspecific.

In experiment 'Cooperation', one potential explanation of the lack of transfers is that our subjects might have perceived the cooperative task as competitive. Differences in bonobos' and chimpanzees' hormonal reactions to social stress might explain why chimpanzees but not bonobos were hindered by the design of the task. Wobber and colleagues (2010) found that chimpanzees exhibited an anticipatory increase in testosterone levels when placed in a situation that led to competition compared to an equal share of food. In contrast, bonobo males showed an increase in cortisol instead of testosterone levels in the former compared to latter situation. As Wobber and colleagues (2010) reviewed, increased testosterone levels have been associated with a higher power motive, while increased cortisol levels with a passive coping-style during competition. We did not include a social training in our experiment, during which subjects could have understood that rewards were equally shared upon successful cooperation. Therefore, even if both species initially perceived our cooperative task as competitive, it might have induced social stress in chimpanzees that prevented them from actually understanding the task. Nevertheless, we also did not find transfers in female chimpanzees during the cooperative task and the pattern of hormonal shifts is not as clear as in males, pointing to a different reaction towards competition between the two sexes (Wobber et al., 2010).

An alternative and not necessarily mutually exclusive explanation is that bonobos might be either more susceptible to begging by conspecifics or better able to interpret such behaviours. Rilling and colleagues (2012) revealed structural brain differences in bonobos compared to chimpanzees that, at least in humans, are involved in emotional contagion, interoceptive abilities, and socio-emotional processing (Critchley et al., 2013; Ormel et al., 2013). These in turn seem to support empathic abilities (Critchley et al., 2013). On the level of overt behaviour, bonobos are also better at solving theory of mind tasks (Herrmann et al., 2010) and pay more attention to facial cues (Kano et al., 2015) than chimpanzees do. Moreover, bonobos are sensitive to whether aggression directed at them was expected in a given social context (Clay et al., 2016). We could show that bonobos compared to chimpanzees also seem to be more altruistically motivated. This gives further support to the notion that structural brain differences seem to translate into differences in overt behaviour and that these brain areas seem to support similar functions in bonobos as in humans.

Our results are in line with previous research that revealed bonobos to be more skilful cooperators than chimpanzees (Hare et al., 2007; Pele et al., 2009). In contrast to previous results (Jaeggi et al., 2010), bonobos were also more willing to act altruistically than chimpanzees. Replicating Jaeggi and colleagues' (2010) study would be helpful to assess whether the differences in results were due to the particular population tested or due to a more general tendency of bonobos and chimpanzees being differently altruistic depending on the context.

B. Do chimpanzees teach?

Chimpanzees also did not teach their naïve partner what motions to perform, even when they could have acquired rewards through their partner's success. Thus far, researchers only assessed teaching behaviour without using instrumentation that allowed measuring precise changes in possible demonstrative action sequences. The Polhemus motion tracker enabled us to assess more subtle cues. Additionally, we sought to understand whether the previous lack of evidence that chimpanzees teach might be due to a lack of motivation to transmit knowledge to others instead of a lack in cognitive capacity.

While the method of using a Polhemus motion tracker worked (i.e. we could show that chimpanzees might have been influenced by response facilitation in experiment 'Independent' and operated their empty apparatus generally less when being occupied collecting eggs in experiment 'Dependent'), we did not find that they modified their behaviours consistent with our expectations of what we thought would constitute teaching. This was true even when we provided an incentive to teach. Thus, this study enabled us to rule out that chimpanzees did not teach because they were not motivated to do so, or because they adapted their behaviours in a very subtle manner that was difficult to detect through video recordings. Our finding confirms previous research.

As was discussed earlier, chimpanzees seem to possess the necessary cognitive abilities to engage in more flexible forms of teaching, namely forming a representation of ignorance in others (Crockford et al., 2012), understanding when another individual holds a wrong belief about situations (Krupenye et al., 2016) or when an individual performs actions that are inadequate to achieve a goal (Call et al., 2005), and using foresight (Bräuer & Call, 2015; Osvath & Osvath, 2008). Krupenye and colleagues (2016) elegantly showed that chimpanzees can anticipate the actions of another individual based on the individual's false belief; however, this ability might not be sufficient to understand how to identify which actions are actually necessary to change the knowledge state of another individual. Even though we do know that chimpanzees emit alarm calls to warn ignorant group members of danger (Crockford et al., 2012), they might not understand how to adapt their own movements in a way that could transmit the missing knowledge. Full-blown theory of mind abilities might support the latter and be lacking in chimpanzees. Additionally, we do not know whether chimpanzees are able to understand that knowledge states can change over time and are not always either present or absent. Both these cognitive abilities would support the identification of the zone of proximal development of another individual and to understand which actions are needed to convey missing pieces of knowledge.

Only Grosse and colleagues (2015) found that in one context chimpanzees possibly realized that actions can be demonstrated with an empty apparatus. One difference between the two studies is that in their study the partner was a human and not a conspecific, as in our experiment. Chimpanzees also seem to solicit the attention of a human but not conspecific partner more readily (Hirata & Fuwa, 2008). This might be due to different expectations towards humans and conspecifics. In both these experiments, the tested populations were exposed to humans from birth onward and, through being tested on a regular basis, gained experience in humans' responsiveness to communication and consequently expect to be rewarded upon solving tasks. In contrast to wild populations that hunt together, these captive chimpanzees might generally not need to communicate in a clear manner to attain common goals. We do not know yet in what ways chimpanzees communicate differently with humans than with chimpanzees and whether this might result in a lack of expectation and consequent lack of motivation to teach (or to perform other behaviours for that matter). Still, experiment 'Dependent' should have at least induced sufficient motivation to try and transmit knowledge to their conspecific.

Future research should 1) address the question of whether Grosse and colleagues' (2015) finding can be replicated in that chimpanzees might teach human partners and 2) whether chimpanzees understand that knowledge states can change instead of being either present or absent. Moreover, advances on theory of mind tasks will give insight into the extent of chimpanzees' theory of mind abilities and whether this could be a limiting factor.

C. How do children teach?

Investigating the developmental trajectory of teaching enables us to understand which abilities are most likely already in place before children display cumulative cultural abilities. We can therefore deduce which cognitive abilities (i.e. in this case which level of teaching capabilities) are crucial to support cumulative cultural abilities, and that any capabilities arising afterwards are not directly needed for the expression of cumulative culture and might just support it later on. Previous research most often included direct instructions and prompts that the child should teach their partner how something works. This will most likely influence not only whether but also how children engage in teaching, thereby making the results less ecologically valid if we want to know how teaching naturally develops. Moreover, studies typically only included a few age groups, which decreases comparability of results across studies. We therefore included children spanning an age from four to seven years and, thus, covered the age range during which most development in terms of teaching strategies seems to occur. Additionally, we assessed how motivational factors influenced whether and how children taught.

We found that children as young as four years old engaged in spontaneous and altruistic teaching without being prompted to do so by the experimenter. In most instances children communicated proactively in the test condition. We did not find a significant increase in whether children engaged in teaching between the two experiments, which corroborates previous findings that children are motivated to help out of other-regarding preferences. Moreover, all age groups were similarly helpful. Children used specific explanations as a teaching strategy the most and independent of whether they benefitted from their help. 7-year-old children never used iconic gestures when they did not benefit from teaching, but started to do so when they could acquire rewards through their partner. Across age groups, we found an increase between experiment 'Independent' and 'Dependent' in relevant communication (i.e. specific and general explanations and iconic gestures) when the partner could make use of the information (i.e. test and expert control condition), while the frequency remained the same when the partner could not make use of the information (i.e. social facilitation control condition). Thus, when children benefitted from their partner correctly operating the apparatus they showed an increase in communicative strategies that directly revealed how the mechanism or task worked. Only the communicative categories feedback and attention getter were exhibited to a comparable degree between the two experiments.

We expected that using an apparatus would grant young demonstrators the advantage to compensate for possible difficulties in successfully explaining what needed to be done. However, even though we observed instances of children that solicited the attention of their partners before operating their apparatus, we did not find statistical evidence that children adapted their motions or manipulated their apparatus more often when facing a naïve partner that needed help. This might be due to the fact that 4-year-olds surprisingly already used all communicative behaviours that we coded. We therefore did not find statistical support for a developmental trajectory of the usage of different teaching strategies. This could either mean that our measurements were not sensitive enough to detect a change in teaching strategies or that our sample size was not big enough. Alternatively, young children that succeeded during training might not be as representative of the entire spectrum of 4-year-olds as in previous studies. Nevertheless, we still show that a sufficient amount of 4-year-olds were able to pass and were also adept at using varied teaching strategies. Given that children younger than 3.5 years did not pass the training, future research could adapt the task slightly to investigate whether these would make more use of their own apparatus and demonstrate the correct actions.

D. Conclusion

In the current studies, we showed that bonobos and human children are willing and able to help another individual without directly benefitting from it. This result could be possibly explained by other-regarding preferences, as both children and bonobos acted differently once the motivation to help became self-centred. Bonobos shared tools more consistently when they benefitted from it (Chapter 2), while children adapted their teaching strategies when they were dependent on their partner's understanding of the task (Chapter 4). Still, both species, respectively, shared tools or taught even when it was clear that no immediate benefits resulted. In contrast, chimpanzees did not share tools (Chapter 2) and nor did they teach even when they could have benefitted from it (Chapter 3).

The study that investigated teaching in children (Chapter 4) was adapted from the study used to assess whether chimpanzees teach (Chapter 3). Due to logistical reasons, we could not retest the children and had to adapt the procedure so that training and testing fitted one test day. Therefore, children received an extensively shortened training protocol and, additionally, we administered less trials during each training phase and test. Most importantly, however, we included verbal introductions for the children but could not do the same for the chimpanzees. Thus, the children had an advantage in that the experimenter verbally introduced the apparatus and explained parts of the mechanics such as the location of the eggs and where they could be picked up. The experimenter also stated that eggs would be lost if they fall into the black box attached to the bottom of the apparatus. Importantly, the experimenter never talked about the specific motions that had to be performed, nor did she instruct the children to teach. Instead, the children were abruptly left alone by the experimenter before the test started as she pretended to receive an important incoming call. We decided to verbally communicate with the children even though this changed the procedure to that of the chimpanzees, given that especially young children might have felt uncomfortable to interact with the apparatus during training without a prior introduction of what the goal of this task is (i.e. retrieve eggs and exchange them for stickers). Moreover, without any form of introduction prior to the test, children would have most likely not started operating the apparatus because they would have been uncertain whether they are allowed to. Furthermore, we tested chimpanzees in separate adjacent cages but for testing children we could not recreate walls to mimic a cage. Thus, we only placed a barrier between the two tables to prevent easy access to the partner's apparatus. To ensure that children did not walk around the table to operate their partner's apparatus, we needed to establish some rules before the experimenter could leave the room. By establishing such rules beforehand, the experimenter did not have to intervene during the test. This more closely resembled testing the chimpanzees. Thus, before the experimenter left the room to answer the urgent incoming phone call she stated the rule to not walk around the table, and said that she would be back soon and they could start playing in the meantime. This ensured that children felt comfortable to start playing, but at the same time they still needed to figure out by themselves what the task encompassed, i.e. that they had to teach their ignorant partner. Therefore, even though a comparison between the two experiments needs to be done with caution, each experiment in itself allowed us to gauge the two species' teaching skills while taking into consideration that they require different test contingencies (i.e. more time during training for chimpanzees and verbal communication before training and test for children)

Another limitation that is inherent to most studies conducted in the laboratory, is that their ecological validity is diminished. In our studies, apes faced an arbitrary apparatus that had no ecological relevance to them. However, the specific populations that we tested were used to solving arbitrary tasks on a daily basis and succeeded in a multitude of them. These apes were aware that rewards could be obtained upon solving tasks presented to them and were generally motivated to do so. We could further show that all individuals of each study understood which actions needed to be performed to retrieve rewards from the given apparatus. Introducing an ecologically irrelevant task might have decreased an intuitive understanding of which responses were required during testing (i.e. helping/cooperating by providing a tool or teaching learned motions), however, we investigated cognitive abilities that grant humans a great advantage exactly for the reason they can be flexibly applied in new contexts and to solve new problems. We indeed showed that already young children started to teach without being instructed to do so or given a proper introduction to the task ahead of them. Thus, they spontaneously engaged in teaching upon encountering a new problem. This was true even though neither the motion sequence nor the apparatuses were familiar to children as well. However, depending on the toys that the children could play with at home, the materials such as plexiglass might have been familiar to them. Such familiarity could have increased an intuitive understanding of the physical properties and internal mechanics of the apparatuses. Consequently, it might have resulted in an enhanced insight into which information were needed by the ignorant partner to comprehend the mechanism. Future laboratory research with chimpanzees could benefit from using a design that resembles naturally occurring behaviours such as stick or stone tool use (refer to Chapter 3 for more detailed discussion on possible avenues). Furthermore, field research is required to obtain a full picture of chimpanzees' cognitive abilities and to understand which behaviours are relevant for navigating their ecological niche.

I reviewed several cognitive abilities that have been proposed to create the foundations on which cumulative culture builds on. Innovation and high-fidelity social learning enable individuals to produce and copy new strategies and solutions that might form the basis of cultural variation between groups. Teaching requires the active involvement of the knowledgeable individual, while cooperative and altruistic tendencies within a social group enable individuals to solve tasks together and can support indirect reciprocity and, thus, other-oriented teaching.

Previous research showed that chimpanzees are able to innovate new solutions and inhibit prepotent responses (Manrique et al., 2013). Moreover, they learn new behaviours through observation and make use of emulation and imitation (Buttelmann et al., 2007; Hopper et al., 2007; Horner & Whiten, 2005; Price et al., 2009). Unfortunately, less is known about bonobos concerning these questions (though see Manrique et al., 2013), and once again shows the gap in our understanding of this species' cognitive ability. Nevertheless, innovation and social learning by themselves seem to not be sufficient to support cumulative cultural evolution.

Teaching in humans is an ability that arises early in ontogeny, that can be flexibly adapted to new problems and that does not seem to be self-motivated. In comparison, current evidence of teaching in nonhuman species has been limited to one specific context for the given species (e.g. feeding, spacial navigation). Nonhuman species' ability to teach does not seem to be applied for teaching or rewarding different skills or responses and seems to arise in response to specific external cues. As was discussed earlier in more detail, meerkats for example respond to the call type of pups and thus adapt their teaching depending on the pups' age and assumed corresponding skill-level (Thornton, 2008; Thornton & McAuliffe, 2006). Similarly, when ants discover a new site all other ants will be naïve and can thus be potential learners (Franks & Richardson, 2006). This shows that teaching can arise as an adaptive response to the environment and possibly without underlying complex cognition, as long as it is tailored to one specific and stable context. In contrast, human teaching occurs in various contexts and through different modalities, such as teaching how to behave in certain situations, how to build complex structures, and even how to teach itself. Hoppitt and Laland (2013) refer to this flexibility as a "generalized capacity for teaching", which has been proposed to have co-evolved with the capacity for cumulative culture (Fogarty et al., 2011). It remains unknown whether differences between the observed behaviours of humans and nonhuman species are of degree or kind and which specific factors might have enabled the evolution for a general ability to teach. However, in comparison to other animals that teach, humans can apply this ability to new problems and even young individuals are able to teach spontaneously without prior instructions (see Chapter 4). This underlines the fact that teaching plays an integral role in human society.

Even though chimpanzees cooperate in different instances in the wild and captivity, it seems that this is not done due to other-regarding preferences. No study to date has produced solid evidence that chimpanzees engage in teaching and the rare observations from the wild cannot rule out likely alternative explanations (discussed in Chapter 3). One reason why teaching is this prevalent in human society might be due to social norms that regulate and reinforce cooperative behaviours. As was previously discussed, gossip, reputation, and third-party punishment are mechanisms that strongly affect the behaviour of others and support indirect reciprocity by creating strong forces to behave altruistically towards others. In our experiment (see Chapter 4), the main experimenter left the room while the second experimenter was seemingly busy. Moreover, children were not prompted to teach in any way. Yet, the anticipation of subsequent interactions with experimenters and caretakers might have affected the children enough that they engaged in teaching to a similar frequency with and without acquiring a benefit from it. In nonhuman great apes, there is currently no evidence of third-party punishment (Riedl et al., 2012, Schlingloff & Moore, 2017). Moreover, chimpanzees do not seem to try to be perceived as cooperative by their group members (Engelmann et al., 2012), even though they themselves select their cooperative partners based on observations of previous interactions (Herrmann et al., 2013). Similarly, chimpanzees observe others in order to learn new skills and make use of complex social learning mechanisms (e.g. Call et al., 2005; Buttelmann et al., 2007; Hopper et al., 2007; Hopper et al., 2008; Horner & Whiten, 2005), but in turn do not seem to actively provide information to others who are observing them.

Limited theory of mind abilities might play a role here as chimpanzees might not be able to reflect upon others' perceptions of themselves and resulting changes in the behaviour of others. Furthermore, advanced language skills enable humans to not only effectively communicate about abstract concepts during teaching episodes but also to gossip about others. Gossip functions as a way to assess and update the reputation of other individuals in addition to observing interactions themselves (Nowak, 2006). In big groups it can therefore buffer against diminished chances of directly observing all interactions. Sommerfeld and colleagues (2007) showed that gossip facilitated indirect reciprocity in an experimental setting, and altruistic responses increased when participants were led to think about corresponding social norms (Krupka & Weber, 2009). Gossip can also be a means to learn and communicate social norms of the respective cultural environment (Noon & Delbridge, 1993). Thus, with the development of language, humans were able to regulate altruistic and cooperative exchanges and form clear punishments for defecting individuals. Nevertheless, social norms could still be enforced without language and through ostracism or physical punishment. A lack of third-party punishment and reputation management might therefore partly explain why we do not find cooperation, and consequently teaching, on a larger scale in nonhuman great apes. However, this conclusion is based on one study and, additionally, we are lacking information on other species such as bonobos. More studies are needed to confirm the lack of third-party punishment and reputation management in closely-related and distantly-related species.

Hill and colleagues (2011) hypothesized that regulated altruistic and cooperative exchanges allowed for more frequent and possibly more tolerant interactions, which in turn increased the chances of observing and socially learning skills or rare innovations. Thus, in such tolerant social structures, the costs of complex social learning mechanisms became outweighed by the benefits and resulted in an accumulation of more complex cultural traditions. In humans, these metagroup social structures possibly allowed groups to form cumulative culture and become fitter than groups that lacked the described social dynamics. Groups that were able to establish cooperation between individuals through altered social dynamics consequently gained a greater overall fitness benefit and outcompeted groups and other species without such cooperative interactions (Nowak, 2006). Taken together, this might have allowed humans to start constructing their niche instead of adapting to it, thereby inhabiting various climates and at some point possibly other planets.

Given that bonobos seem to be more adept at solving cooperative tasks and altruistically help one another, they might be a candidate species to investigate their teaching abilities in more detail. We showed that bonobos outperformed chimpanzees on a cooperative task and even helped their partner out of other-regarding preferences (see Chapter 2). Their enhanced social tolerance could create more chances to closely observe other group members, thereby increasing chances to observe and socially learn new innovations. While chimpanzees become increasingly intolerant of adult group members especially when food is involved, bonobos retain their social tolerance even between unrelated adult group members. Thus, they can more freely interact with others at a time that their physical cognition and understanding about relationships between inanimate objects is at its peak. This could create an advantage compared to chimpanzees in that they can understand and socially learn what other adult group members are doing and possibly build upon the acquired knowledge, which subsequently could be again transmitted to other adult group members. Future studies should therefore include bonobos when assessing cumulative cultural abilities in nonhuman primates.

Moreover, they should make efforts to shift their focus from teaching of tool use skills towards including other behaviours for which offspring or group members would benefit from teaching. In the wild, bonobos show less propensity to use tools (Furuichi et al., 2015; Hohmann & Fruth, 2003; Ingmanson, 1996; Kano, 1982) compared to chimpanzees (McGrew, 2004; Whiten et al., 1999). While some studies suggest that bonobos are less proficient on tasks involving tool usage and physical causality (Herrmann et al., 2010) and have less intrinsic motivation to engage with objects (Koops, Furuichi, & Hashimoto, 2015) than chimpanzees, others did not find a difference between the two species in terms of apprehending functional properties of tools and the variety of contexts in which individuals use tools (Herrmann, Wobber, & Call, 2008; Gruber, Clay, & Zuberbühler, 2010). More extensive reports from the wild that include several bonobo populations are needed to understand whether reported differences in tool use frequency are generally true on a species level or merely reflect population differences within the species. It could therefore be worthwhile to extend the search of potential teaching away from merely investigating tool use skills and towards behaviours such as spacial navigation, food consumption, or even gestural communication. These in turn could also be candidate behaviours to assess whether bonobos might exhibit rudimentary cumulative cultural abilities. As was discussed before (see Chapter 1), ungulate species and pigeons cumulatively adapted feeding or homing paths, respectively. Such findings call for a necessity to not only focus on one aspect of animals' social life but broaden the search and, thus, understanding of cumulative culture.

It seems that cumulative culture is supported by a multitude of cognitive abilities such as to innovate, emulate and imitate, cooperate, and teach. Focusing on our closest living relatives enables us to verify which of the proposed cognitive abilities are crucial for the expression of cumulative culture. Even though our closest living relatives possess cultural variation across groups of the same species, no evidence has been produced so far that they possess the ability of cumulative culture (Tennie et al., 2009). Taking the discussed studies and previous research together, different species across the animal kingdom have the capacity of some of the proposed cognitive abilities. However, it seems that the only species that engages in teaching upon facing a new task are humans. Therefore, out of the four cognitive abilities that create the foundations on which cumulative culture builds on, the ability to teach flexibly in conjunction with the other cognitive abilities seems to be the specific ability crucial for the expression of cumulative culture instead of culture itself (e.g. cultural variation). Social mechanisms such as social norms, third-party punishment, and the resulting regulated cooperative interactions, could have influenced the scale in which cooperation and teaching is seen in humans and possibly explains why humans became such an invasive and evolutionarily speaking successful species.

VI. References

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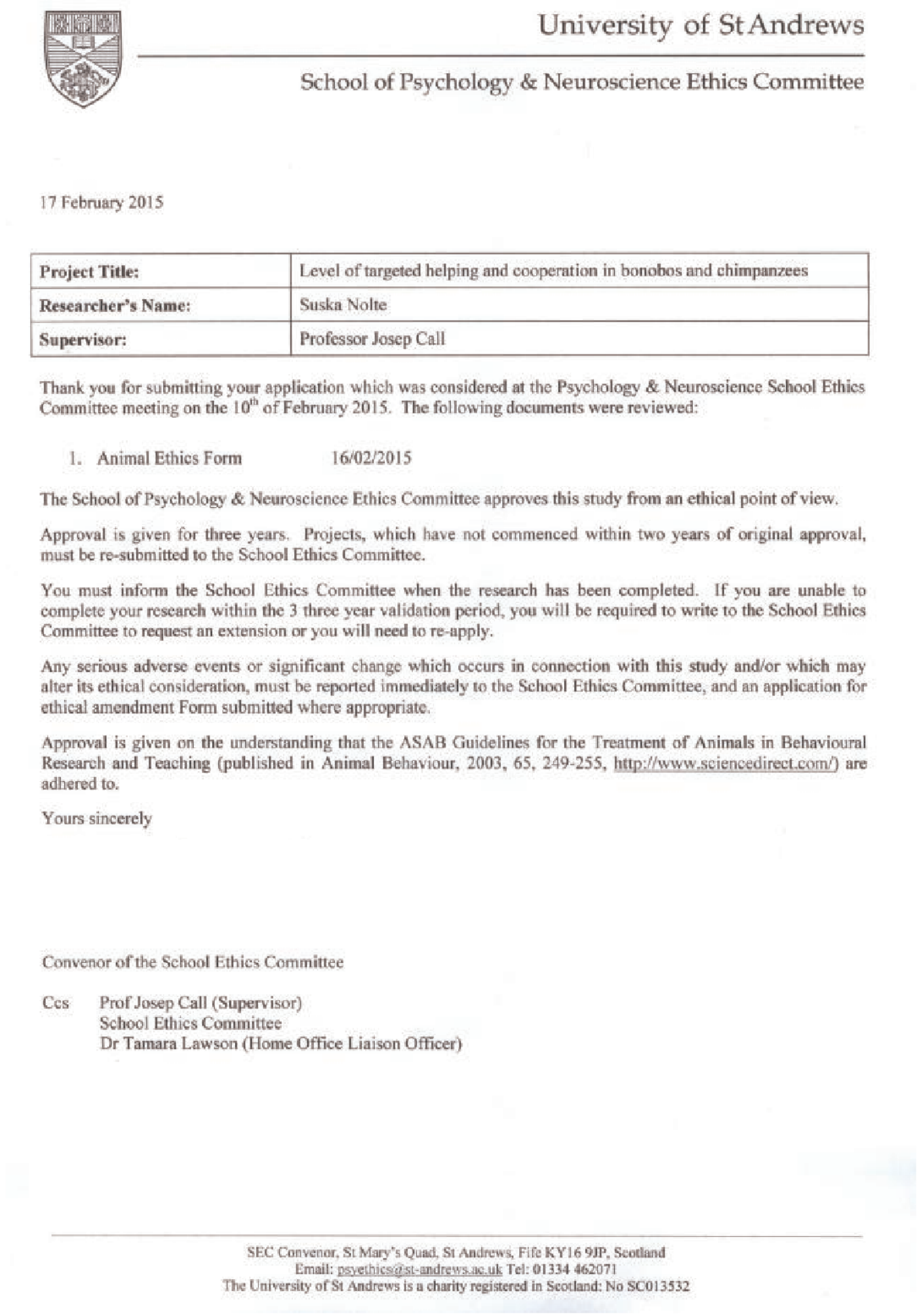
VII. Appendix

1. Ethics Approval, Targeted Helping and Cooperation (Chapter 2)



University of St Andrews

School of Psychology & Neuroscience Ethics Committee

17 February 2015

Project Title:	Level of targeted helping and cooperation in bonobos and chimpanzees
Researcher's Name:	Suska Nolte
Supervisor:	Professor Josep Call

Thank you for submitting your application which was considered at the Psychology & Neuroscience School Ethics Committee meeting on the 10th of February 2015. The following documents were reviewed:

1. Animal Ethics Form 16/02/2015

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

Approval is given for three 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 3 three 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 (published in Animal Behaviour, 2003, 65, 249-255, http://www.sciencedirect.com/) are adhered to.

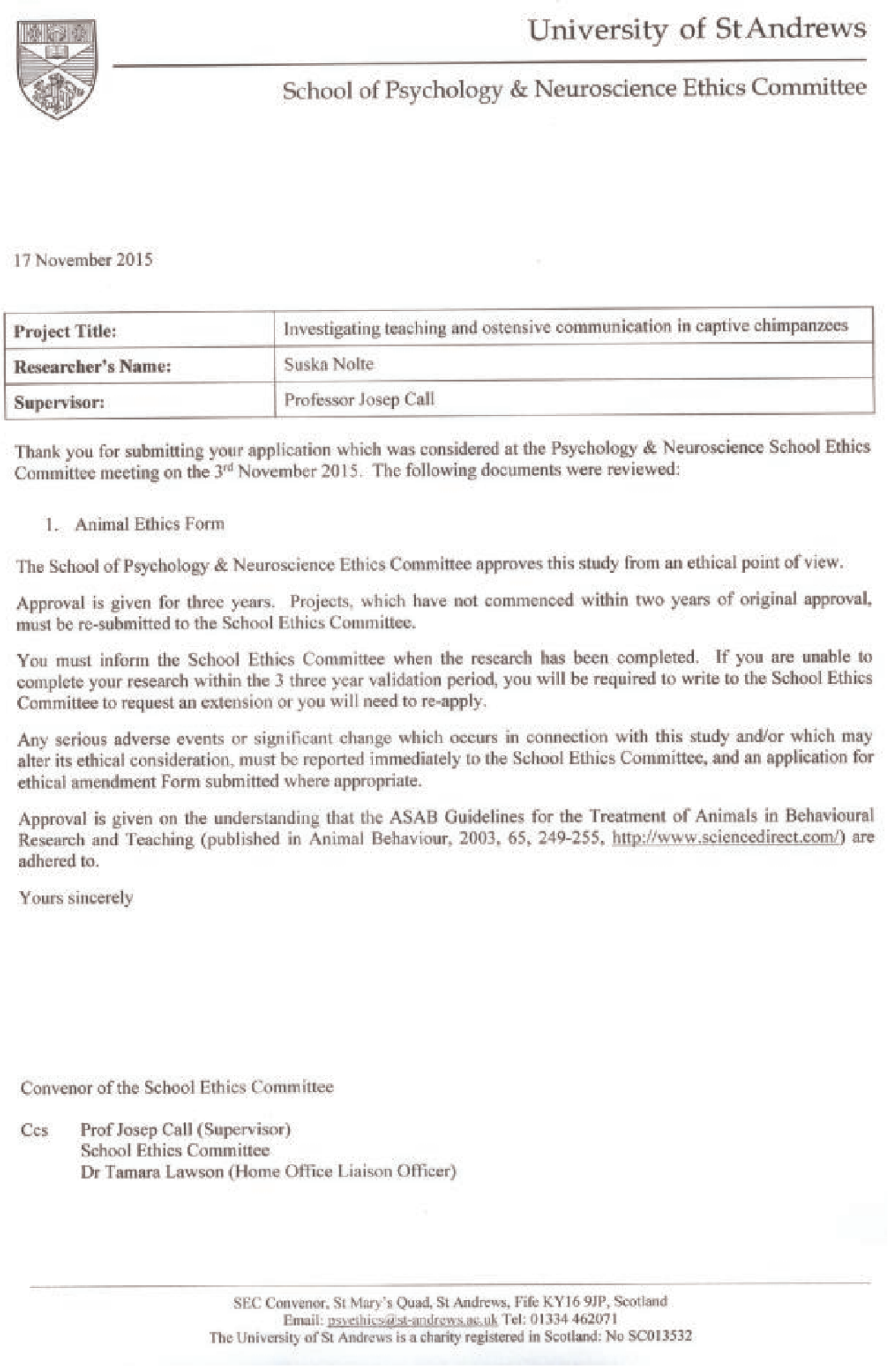
Yours sincerely

Convenor of the School Ethics Committee

Ccs Prof Josep Call (Supervisor)
School Ethics Committee
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

2. Ethics Approval, Teaching in Chimpanzees (Chapter 3)



University of St Andrews

School of Psychology & Neuroscience Ethics Committee

17 November 2015

Project Title:	Investigating teaching and ostensive communication in captive chimpanzees
Researcher's Name:	Suska Nolte
Supervisor:	Professor Josep Call

Thank you for submitting your application which was considered at the Psychology & Neuroscience School Ethics Committee meeting on the 3rd November 2015. The following documents were reviewed:

1. Animal Ethics Form

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

Approval is given for three 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 3 three 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 (published in Animal Behaviour, 2003, 65, 249-255, http://www.sciencedirect.com/) are adhered to.

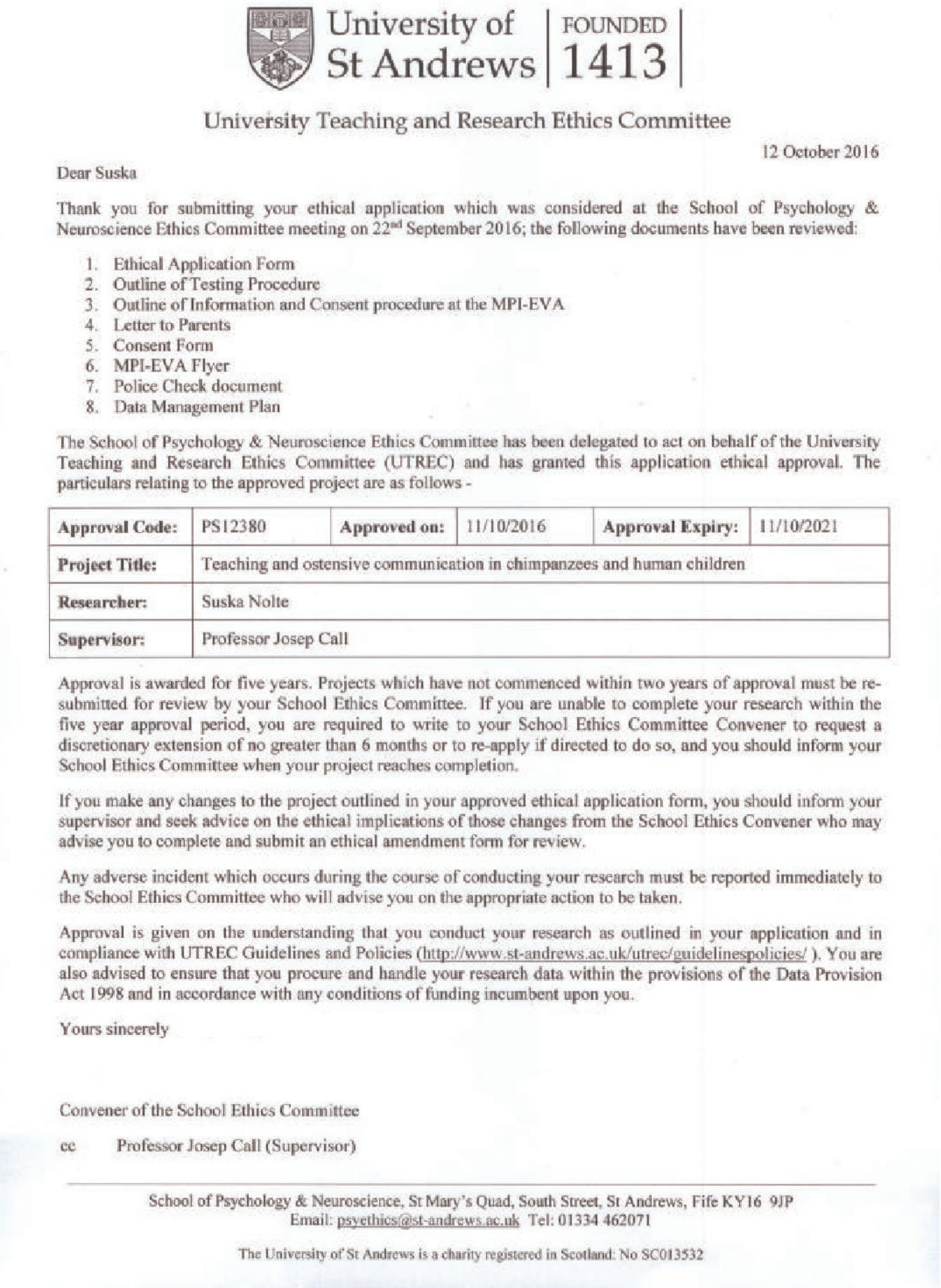
Yours sincerely

Convenor of the School Ethics Committee

Ccs Prof Josep Call (Supervisor)
School Ethics Committee
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

3. Ethics Approval, Teaching in Children (Chapter 4)



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University Teaching and Research Ethics Committee

12 October 2016

Dear Suska

Thank you for submitting your ethical application which was considered at the School of Psychology & Neuroscience Ethics Committee meeting on 22nd September 2016; the following documents have been reviewed:

1. Ethical Application Form
2. Outline of Testing Procedure
3. Outline of Information and Consent procedure at the MPI-EVA
4. Letter to Parents
5. Consent Form
6. MPI-EVA Flyer
7. Police Check document
8. Data Management Plan

The School of Psychology & Neuroscience Ethics Committee has been delegated to act on behalf of the University Teaching and Research Ethics Committee (UTREC) and has granted this application ethical approval. The particulars relating to the approved project are as follows -

Approval Code:	PS12380	**Approved on:**	11/10/2016	**Approval Expiry:**	11/10/2021
Project Title:	Teaching and ostensive communication in chimpanzees and human children				
Researcher:	Suska Nolte				
Supervisor:	Professor Josep Call				

Approval is awarded for five years. Projects which have not commenced within two years of approval must be re-submitted for review by your School Ethics Committee. If you are unable to complete your research within the five year approval period, you are required to write to your School Ethics Committee Convener to request a discretionary extension of no greater than 6 months or to re-apply if directed to do so, and you should inform your School Ethics Committee when your project reaches completion.

If you make any changes to the project outlined in your approved ethical application form, you should inform your supervisor and seek advice on the ethical implications of those changes from the School Ethics Convener who may advise you to complete and submit an ethical amendment form for review.

Any adverse incident which occurs during the course of conducting your research must be reported immediately to the School Ethics Committee who will advise you on the appropriate action to be taken.

Approval is given on the understanding that you conduct your research as outlined in your application and in compliance with UTREC Guidelines and Policies (http://www.st-andrews.ac.uk/utrec/guidelinespolicies/). You are also advised to ensure that you procure and handle your research data within the provisions of the Data Provision Act 1998 and in accordance with any conditions of funding incumbent upon you.

Yours sincerely

Convener of the School Ethics Committee

cc Professor Josep Call (Supervisor)

School of Psychology & Neuroscience, St Mary's Quad, South Street, St Andrews, Fife KY16 9JP
Email: psyethics@st-andrews.ac.uk Tel: 01334 462071

The University of St Andrews is a charity registered in Scotland: No SC013532