Perspective-Taking and Theory of Mind in Great Apes

Der Fakultät für Biowissenschaften, Pharmazie und Psychologie

der Universität Leipzig

eingereichte

DISSERTATION

zur Erlangung des akademischen Grades

Doctor rerum naturalium

(Dr. rer. nat.)

vorgelegt

von Dipl.-Biol. Heinz Gretscher

geboren am 10.02.1978 in Saarlouis

Leipzig, den 6. April 2017

BIBLIOGRAPHISCHE DARSTELLUNG

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Perspective-taking and Theory of Mind in Great Apes

Fakultät für Biowissenschaften, Pharmazie und Psychologie

Universität Leipzig

Dissertation

204 Seiten, 308 Literaturangaben, 14 Abbildungen, 13 Tabellen

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Individuals endowed with a ‘Theory of Mind’ (‘ToM’) understand themselves and others as agents whose actions are driven by unobservable psychological states. How and when human infants come to such an understanding has been extensively researched in the visual domain. In my dissertation, I addressed three gaps in the extant literature about what great apes’ know about others' visual perceptions and perceptual beliefs.

In study 1, I investigated orangutans’ understanding of visual attention and others’ visual perspectives in a competitive situation. Overall, the results suggest that orangutans have a limited understanding of others’ perspectives, relying mainly on cues from facial and bodily orientation and *egocentric rules* when making perspective judgements.

In study 2, I explored whether apes and 20 month old human infants requesting a desired object from a human experimenter would use communicative means to direct visual attention towards the object. While infants used pointing to alter the experimenter’s focus of attention, we found no evidence that apes’ employ their point gestures in this way.

In study 3, I examined chimpanzees’ and 5.5 year old human children’s understanding of perceptual beliefs. By designing two novel false belief tasks which required reduced executive functioning, I attempted to find out whether chimpanzees’ historical failure in explicit false belief tasks was due to their lack of *inhibitory control*. Neither the chimpanzees nor the 5.5 year-olds succeeded in the novel tasks.

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Acknowledgements

I am very grateful to my supervisors Prof. Dr. Daniel Haun, Prof. Dr. Katja Liebal and Dr. Juliane Kaminski for providing me with the opportunity to conduct the exciting research presented here, their scientific support as well as their patience with me taking my time to finish this thesis.

Many thanks also to all the other people who directly contributed to this thesis throughout several stages of the data acquisition: Sebastian Tempelmann, Johannes Großmann, Astrid Heck, Antje Girndt, and Lena Rosenbaum for their help with apparatus construction and data collection, Antje Girndt, Laura Damerius, Sarah Bitzmann, and Luisa Hetmann for reliability coding, and Roger Mundry for his valuable statistical advice. Thanks also to 'Katemangostar' and 'Freepik' for providing free collections of animal and fruit icons on Freepik.com that I modified for usage in Figures 10, 11 and 13.

Further, I would like to express my gratitude to the VolkswagenStiftung, Germany, for funding my PhD work as part of the project "Evolutionary Roots of Human Social Interaction (ROSI)", to Biruté M. F. Galdikas and the Indonesian Ministry of Research and Technology (RISTEK) as well as Lilly Ajarova and the Ugandan National Council for Science and Technology and the Uganda Wildlife Authority for granting me permission to do research in their facilities. I would also like to thank the child lab team of the Max Planck Institute for Evolutionary Anthropology as well as the keeper staff of the Leipzig zoo, the Orangutan Care Centre and Quarantine in Pasir Panjang, and the Ngamba Island Chimpanzee Sanctuary for their friendly support in handling participants as well as in various administrative matters.

Many thanks also to Nathan Pyne–Carter, Juliane Kaminski, Marie Schäfer, Mike Chase, and Katja Liebal for reviewing and proofreading parts of my manuscript.

Beyond scientific work in itself, special thanks to Nadja Richter, Marie Schäfer, Antje Girndt, Sebastian Schütte, and all the other CoCoA and ROSI members for providing a very inspiring and enjoyable working atmosphere. Special thanks also to my flatmates Christel Schneider, Astrid Heck, Andreas Richter, Katharina Kullmann, Cesare de Filippo, Marie Schäfer, Grit Schubert, Martin and Nina Surbeck and Arvid and Marilyn Lürtzing for providing an equally enjoyable atmosphere at home. Many thanks also to all my other friends, who without hesitation always granted support in difficult times and celebrated with me moments of joy. Without all of you, live would be so much less fulfilling!

Last but far from least, I would like to express my special gratitude to my parents Verena and Werner Gretscher, for their continuous support, their enduring patience and infinite trust, without which I would never had been able to pursue my academic education.

1. General Introduction

> After Luit and Nikkie [two chimpanzees competing for group leadership] had displayed in each other's proximity for over ten minutes a conflict broke out between them in which Luit was supported by Mama and Puist. Nikkie was driven into a tree, but a little later he began to hoot at the leader [Luit] again while he was still perched in the tree. Luit was sitting at the bottom of the tree with his back to his challenger. When he heard the renewed sounds of provocation he bared his teeth [indicating fear and submission] but immediately put his hand to his mouth and pressed his lips together. . . . I saw the nervous grin appear on his face again and once more he used his fingers to press his lips together. The third time Luit finally succeeded in wiping the [fear] grin off his face; only then did he turn around. (de Waal, 2007, p. 128)

When 'hiding' his facial expression, did Luit consider that turning around would have caused his challenger to *see* his fear grin, letting Nikkie *know* that Luit was *afraid*? Did Luit avert his face because he thought that by doing so Nikkie would remain *ignorant* about his fear, ultimately leading his opponent to the *false belief* that Luit was confident he would emerge victorious from any fight? Or had Luit—without reasoning about Nikkie's mental states—simply learned to avoid impeding aggression by not openly presenting his bared teeth to adversaries?

In exploring these kind of questions, Premack and Woodruff (1978) coined the term 'Theory of Mind' (henceforth 'ToM') denoting thereby individuals who understand themselves and others as agents whose actions are driven by unobservable mental states which might be different from their own (and the 'true' state of affairs). To investigate whether adult humans, who frequently *mentalize*, share this capacity with their closest living relative, Premack and Woodruff (1978) presented Sarah, a female chimpanzee trained in sign language, videotapes showing a human actor struggling to solve various problems (e.g., trying to attain food that was out of reach or attempting to escape from a locked cage). Sarah then had to choose between two photographs—with one constituting a solution to the videotaped situation (e.g., a photograph of the human using a rod to retrieve the food or a photograph of a key) and the other which did not. Sarah significantly chose the correct one of the two alternatives, suggesting that she understood something about the actors' intentions (cf. Savage-Rumbaugh, Rumbaugh, & Boysen, 1978).

Premack and Woodruff's seminal study initiated a plethora of ToM research. To comprehend what skills amount to a ToM, scientists have teased apart this capacity by analysing individuals' understanding of certain aspects of other minds, such as goals, intentions, desires, emotions, (visual) perceptions, knowledge, ignorance, and (false) beliefs. While some researchers have focused on examining at what age human infants and children start to exhibit these respective understandings, others have studied whether or not these cognitive skills can also be found in other animals.

Nevertheless, almost 40 years later, the lively debate about whether a ToM is unique to humans or whether, and to what degree, we share this capacity with nonhuman primates and other animals is still ongoing. Sceptics argue there is no need to postulate an understanding of *mental states* in nonhuman primates and other animals as their performance can be explained equally well (and more parsimoniously) by assuming they are operating via learned (and innate) rules, based solely on cues arising from externally perceivable behaviour patterns (e.g., Povinelli & Vonk, 2003, 2004). As 'mind reading' also requires overt contextual information to some extent, it is virtually impossible to rule out criticism of this kind on the basis of a single experiment. However, if members of a given species successfully solve various novel problems related to the understanding of a certain mental state, it might be more parsimonious to assume that they understand the common underlying mental state than postulating that they solve each problem with a unique set of behavioural rules (Whiten, 1996).

The current thesis sets out to contribute to the ongoing debate on whether or not the human ToM constitutes a unique phenomenon. I will investigate non-human great apes' (henceforth 'great apes') understanding of others' visual perceptions and visual attention, as well as their understanding of others' false beliefs, in a variety of communicative and competitive situations. First, I will give a short overview about human infants' and great apes' understanding of others' minds (Chapter 1). In particular, I will provide information about the development of various human mind reading skills throughout infancy and childhood. Further, I will present several theories of how these skills might have evolved and show how comparing the performance of different species in a cognitive task can help in disentangling the evolutionary trajectories of the respective cognitive trait. Subsequently, I will briefly summarize what is known about great apes' social lives and social cognitions. In the final part of the current chapter, I will introduce my own research. In Chapters 2–4, I will present three empirical studies that I conducted to investigate great apes' understanding of others' visual perceptions and false beliefs. In the final part of this thesis (Chapter 5), I will summarize the results of these studies and contextualize them (as well as other recent research on great ape social cognition) in two novel theories of human ToM development. In addition, I will discuss the importance of joint attention in the development of ToM, as well as its potential role in observed differences in human and great ape ToM. I will conclude by highlighting limitations of the current thesis arising from the sample composition of my experimental studies.

1.1 Human ToM Development

In typically developing humans a fully fledged ToM is not present from birth but unfolds gradually during ontogeny within the first 4–5 years of life (Bartsch & Wellman, 1995; Wellman & Liu, 2004). Already within their first year of life, human infants show a basic understanding of goals and intentions. For instance, Woodward (1998) habituated (by repeated exposure) 5-month-olds to a scene in which a person reached for an object at a specific location while ignoring a second object at another location. In probe trials, in which the objects' locations were reversed, the infants reacted more surprised (inferred from longer looking times) if the person reached for the same location with the alternative object than when the person reached for the same object at the new location (indicating that they perceived the former situation as more dissimilar to the habituated one). Thus, the infants apparently perceived the person's reaching goal as more relevant than the exact movement patterns (see Phillips & Wellman, 2005 for a similar result). Behne, Carpenter, Call, and Tomasello (2005) found that infants at 9 months of age discriminate between a person that is unwilling to hand over a toy, and a person that is unable to do so (e.g., due to a failed attempt). In addition, when copying a demonstrated action, 14–18 month old infants are more likely to do so if the action was intended than when it occurred accidentally (Carpenter, Akhtar, & Tomasello, 1998). Research also indicates that from 12 months of age, infants reproduce a demonstrated action more consistently if the action is executed voluntarily, rather than under physical constraints (Gergely, Bekkering, & Király, 2002; Schwier, van Maanen, Carpenter, & Tomasello, 2006); and then when observing the demonstration of a failed action, 15-month-olds have been found to copy the intended goal of the action (Johnson, Booth, & O'Hearn, 2001; Meltzoff, 1995). Collectively, these data suggests that infants develop a profound understanding of others' goals and intentions within the first 1.5 years of life.

By eighteen month infants are judged to understand that others can have different preferences than themselves (Repacholi & Gopnik, 1997). Irrespective of their own desires, 2-year-olds are able to predict behaviour based on others' desires and assign happy and sad emotions to outcomes corresponding to the fulfilment and dissatisfaction of the respective desire (Rakoczy, Warneken, & Tomasello, 2007; Wellman & Woolley, 1990).

Most research about the development of the understanding of others' perceptions has focused on the visual domain. Infants at an age of 6 months follow the gaze of others to targets within their own visual field (e.g., Butterworth & Cochran, 1980), but by 12 months they are also able to follow the gaze of others to 'out-of-sight' targets (Deák, Flom, & Pick, 2000), behind visual barriers (Moll & Tomasello, 2004), and check back with the looker if they do not encounter a potential gaze target (Carpenter, Nagell, & Tomasello, 1998); suggesting that infants understand the gazing of others as 'seeing'. Around the age of 9–12 months infants also engage in a variety of triadic behaviours related to sharing visual experiences with others (joint attention), such as looking back and forth between the focal object and the eyes of the social partner, and attracting and directing others' visual attention through communicative means as means of giving, showing and pointing (Carpenter, Akhtar, et al., 1998).

While infants at the end of their first year of life already show a profound awareness of whether others share their own focus of attention, only in their second year of life do they begin to demonstrate a more general understanding of what others can and cannot see from their perspective (level-1 visual perspective-taking; Flavell, 1992). In a study by Moll and Tomasello (2006), 24-month-olds observed an adult searching for something in a room that contained two objects—one hidden behind a visual barrier from the adult's (but not their own) sight and a second one out in the open. When prompted to help the adult finding the sought-for object they preferentially handed her the hidden object (whereas they had no preference to give the hidden object in a control condition). If prompted to hide an object from an adult, 2.5 year old infants successfully place the object behind an already present barrier, such that the adult cannot see it, and 3-year-olds additionally succeed at interrupting the adult's line of sight by correctly placing a barrier in relation to the already present (and initially visible) object (Flavell, Shipstead, & Croft, 1978).

Somewhat unintuitive, preceding the understanding of what others can and cannot see, infants already recognize what others know and do not know (i.e., have and have not seen in the past) at an age of 12 months (for a potential explanation see below). Twelve-month-olds point less frequently to the location where an object has fallen after a searching adult had previously observed the event than when he had not (Liszkowski, Carpenter, & Tomasello, 2008). In a study by Tomasello and Haberl (2003), infants at the age of 12 and 18 months played with three novel objects. They jointly engaged in action with the experimenter with two of the objects, while they engaged with the third object with another adult in the experimenter's absence. Subsequently, all three objects were arranged on a tray in front of the infants and the experimenter reacted with excitement when returning, exclaiming 'Wow! Look! Look at that one'. Upon request 12 and 18 month old infants preferentially handed over the object that was novel for the experimenter (see also Moll, Koring, Carpenter, & Tomasello, 2006; Moll, Richter, Carpenter, & Tomasello, 2008). Infants' early sensitivity to shared visual experiences and the cognitively more demanding nature of contrasting the own current perspective with another one might explain why infants' understanding of what others have seen in the past precedes their understanding of others' current perspectives (Moll & Meltzoff, 2011b). Indeed Moll and Tomasello (2007b) found that 14-month-olds, in the Object Request Paradigm of Tomasello and Haberl (2003), failed to acknowledge which of the three objects were familiar to the experimenter if they only observed the experimenter playing with the objects from afar or if the experimenter observed them playing with the objects (i.e., joint engagement appeared mandatory).

The understanding of *how* others perceive objects (level-2 perspective-taking; Flavell, 1992) seems to be even more demanding than judgements about what others currently perceive and does not emerge before 3 years of age. At this age infants recognize how looking through a colour filter will change others' perception of two same-coloured objects (Moll & Meltzoff, 2011a). In the same study, 3-year-olds additionally demonstrated that they understand where in relation to the colour filter an object needs to be placed so that it is seen by the other in a certain colour (i.e., by placing a blue object behind a yellow screen to make it look green, and placing it in front of the screen to make it look blue). However, in other—presumably more challenging—perspective tasks requiring infants to confront their own perspective with that of another, 3 year old children fail while 4–5-year-olds succeed predominantly (Flavell, Flavell, Green, & Wilcox, 1980; Masangkay et al., 1974; Pillow & Flavell, 1986).

Also around the age of 4 years, children start to understand that others' can hold false beliefs that deviate from their own knowledge and perception of of reality (reviewed in Wellman, Cross, & Watson, 2001). For instance, in the location change task ('Sally-Anne task', 'Maxi test') infants observe an agent positioning an object in a hiding place before leaving the room (Baron-Cohen, Leslie, & Frith, 1985; Wimmer & Perner, 1983). During the agent's absence, another individual relocates the object to a different hiding place. If asked where the returning agent will look for the object, children younger than 4 years expect the agent to search for the object in the new location while older infants correctly predict that the agent will search the original hiding place. In the unexpected content task ('Smarties test') a Smarties® tube is presented to the children who are subsequently asked what they believe is inside the tube (Perner, Leekam, & Wimmer, 1987). Assuming that the tube holds Smarties, it is revealed to the children that in fact it contains pencils. When asked what naïve others would believe to be inside the tube, 3 year old children answer that others would believe that the tube holds pencils. Further, they also state that they themselves originally thought that the tube contained pencils. In contrast, most 4-year-olds give correct answers to both questions. Four-year-olds also actively manipulate others' beliefs by deceptively pointing to false targets (J. Russell, Mauthner, Sharpe, & Tidswell, 1991; Sodian, 1991) and producing misleading trails (Sodian, Taylor, Harris, & Perner, 1991). However, more recent research indicates that an implicit understanding of others' beliefs might already be present from around 7–15 months of age (e.g., Kovács, Téglás, & Endress, 2010; Onishi & Baillargeon, 2005; Surian, Caldi, & Sperber, 2007), and that younger infants failure to succeed in explicit tasks might be related to deficits in executive function and inhibitory control (Qureshi, Apperly, & Samson, 2010; Rakoczy, 2010; Sabbagh, Xu, Carlson, Moses, & Lee, 2006). Although cross cultural studies have revealed variation in the developmental trajectories of ToM traits, the capacity itself seems to be universally present across cultures (e.g., Duh et al., 2016; Liu, Wellman, Tardif, & Sabbagh, 2008; Wellman et al., 2001) suggesting an underlying biological and evolutionary basis.

1.2 The Evolution of Social Intelligence

Social intelligence refers to a set of skills allowing individuals to successfully manage social relationships and environments (Ganaie & Mudasir, 2015). In this regard, being endowed with a ToM is evolutionary advantageous as it allows for flexible interpretations and predictions of others' behaviour without the necessity to previously experience the respective agent's reaction in a similar situation. However, as beneficial as this capacity might be it surely does not come for free. It needs to be rooted in neuronal structures, and brain tissue is metabolically expensive (Isler & van Schaik, 2006; Mink, Blumenschine, & Adams, 1981). Thus, such a capacity is only expected to evolve under a specific set of favouring circumstances.

On the basis of the finding that humans and other primates have larger brains in relation to their body size (e.g., Byrne, 1994; Passingham, 1981) and better developed cognitive skills than most other species, many theories have been developed to explain how primate intelligence might have evolved. While some of these theories see the possible causes in the physical domain (e.g., tool use and manufacture: Byrne, 1997; extractive foraging strategies: Clutton-Brock & Harvey, 1980; Milton, 1988), most researchers see social environments as the main driving selective pressure on the evolution of primate intelligence. Latter hypotheses, subsumed under the label of 'social intelligence theory', gain support from the finding that group size correlates with neocortical volume in primates (Dunbar, 1992; Sawaguchi & Kudo, 1990) other mammalian taxa as carnivores (Dunbar & Bever, 1998) and ungulates (Pérez-Barbería & Gordon, 2005). While all social intelligence theories agree the complexity of primate sociality has been pivotal in shaping primate cognition, they vary in regard to what specific aspects of social life have been decisive.

Dunbar (2003) points out that while group life can be beneficial by decreasing predatory pressure (due to increased chances to detect predators) it comes at the cost of increased competition for limited resources. Group members minimize these costs by forming alliances with each other (maintained in many primate species by social grooming). To effectively consolidate one's position within a group it is not only important to successfully manage a set of own alliances, but it is also quintessential to keep track of the inter-individual relationships between other group members. This need in turn potentially promoted the evolution of social cognitive skills that enable individuals to keep track of 'third-party' relations. As the number of third-party relationships increases exponentially with group size so does cognitive demand being reflected by the neocortex volume.

Other factors that enhance social complexity might further increase the selective pressure for socio-cognitive capacities. For instance, living in social groups involving high levels of fission-fusion dynamics (i.e., groups that frequently change over time in size and composition due to individuals continually forming new sub-groups) presumably demands more sophisticated capacities to extract, process and store social information relating to other group members due to the patchy and dispersed nature of inter-individual contacts in fission-fusion groups (Aureli et al., 2008). Indeed Amici, Aureli, and Call (2008) found primates living in fission-fusion groups performed better in tasks measuring inhibitory control—a cognitive skill allowing to override prepotent (behavioural) responses—which is thought to be crucial in the development of the human adult ToM (e.g., Qureshi et al., 2010; Rakoczy, 2010; Sabbagh et al., 2006).

In their ‘Machiavellian intelligence theory’, Byrne and Whiten (1988, 1997) also see within-group competition as driving the evolution of primate intelligence. However, their focus lies more on the underlying mechanics of inter-individual competition within a group. According to them, within-group competition for scarce resources promoted the evolution of social cognitive skills that served individuals to manipulate, exploit and deceive other group members for their own benefit. These skills subsequently led to the evolution of social cognitive skills enabling individuals to counter these manipulative strategies, which in turn reinforced the selective pressure to evolve even more sophisticated skills to out-wit others, and so on (see also Humphrey, 1976). This putative feedback loop is, theoretically, only limited by the expensive nature of neocortical tissue.

While the theories above highlight the competitive aspects of group living as selective pressure on the evolution of primate intelligence, others identify within-group cooperation as a decisive factor (e.g., Brosnan, Salwiczek, & Bshary, 2010; McNally, Brown, & Jackson, 2012). Indeed, sophisticated forms of cooperation have been found in primates—one of the most prominent examples being chimpanzee group hunting (Boesch & Boesch, 1989) in which participants supposedly assume complementary roles as ‘driver’, ‘blocker’ and ‘ambusher’ of prey (cf. Moll & Tomasello, 2007a). Cooperation amongst non-kin individuals is prone to cheating which results in a *fitness loss* to the cooperator and a *fitness benefit* for the defector and thus ultimately in a breakdown of cooperative behaviours (Boyd & Richerson, 1988). To discriminate defectors from good partners, it certainly is advantageous to possess socio-cognitive skills providing insight into others’ (true) intentions and goals (which is a prediction in line with the Machiavellian intelligence theory). Likewise, these skills are useful in coordinating collaborative efforts amongst partners, especially if the cooperation necessitates collaborators to assume complementary roles (Moll & Tomasello, 2007a). As reciprocal cooperation often involves long temporal delays between cooperative interactions, cooperators presumably also need to have a certain degree of inhibitory control at their disposal to be able to suppress the temptation of gaining a short term benefit of defecting, rather than waiting for the potential future reward of a cooperative investment (Aguilar-Pardo, Martínez-Arias, & Colmenares, 2013). The fact that reciprocity is not a widespread phenomenon amongst nonhuman animals (whereas cooperation in general is rather common), however, raises the question whether all these cognitive capacities do arise as adaptations from the selective pressures related to cooperation, or whether they rather constitute prerequisites enabling the emergence of more complex forms of cooperation (Stevens, Cushman, & Hauser, 2005).

It is impossible to evaluate which of the theories mentioned above holds the greatest explanatory power on the basis of a single species (although they do not necessarily exclude each other and might in fact constitute complementary hypotheses). To elucidate the evolution of primate social intelligence it is therefore necessary to compare socio-cognitive skills of a variety of taxa, taking into account their degree of relatedness as well as the details of their social life.

1.3 The Comparative Approach

One difficulty related to the investigation of cognitive traits is that they are not directly observable and must be inferred from behaviour. This can lead to false positive results if the studies designed to test the cognitive trait lack appropriate controls to rule out more ‘simple’ explanations for the observed behaviours, as well as false negative results if the experimental setup lacks ecological validity (Hare, 2001). For instance, paradigms aimed at unveiling socio-cognitive skills of chimpanzees tend to yield a more successful performance if they are embedded within a competitive context than within a cooperative-communicative context (Hare & Tomasello, 2004). This is presumably due to the competitive nature of primate social groups. Though behavioural observations from the field can give a very good first indication of what situation might be most appropriate to elicit a certain cognitive trait it is usually far from obvious which context might be ideal to do so. Therefore, when investigating a cognitive trait, it is of crucial importance to conduct a variety of paradigms embedded in differing contextual situations.

However, to fully understand a complex behavioural or cognitive trait it is not only essential to comprehend its mechanistic details (i.e., how it works) but it is also crucial to understand its evolutionary history (Tinbergen, 1963). Like anatomical structures, behaviour and underlying cognitive capacities can be subject to natural selection whereby existing traits are transformed such that they become better adapted to the respective selective pressures. Traits can be similar across different species if they are closely related and share a common ancestor endowed with the respective trait (homology) or due to convergent evolution caused by similar selective pressures (homoplasy). For instance, it has been discovered that, similar to primates, various vertebrate taxa that live in complex social groups exhibit an increased neocortex ratio in comparison to closely related taxa who live solitary or in smaller or less stable social groups (bats: Barton & Dunbar, 1997; birds: Burish, Kueh, & Wang, 2004; carnivores: Dunbar & Bever, 1998; cetaceans: Marino, 1996).

A difficulty in investigating the evolution of behavioural and cognitive traits is that, contrary to anatomical structures, it is hardly possible to trace back their history based on a fossil record. Thus, to illuminate the evolutionary history of such traits, it is necessary to conduct comparisons amongst closely related species. On the basis of the presence or absence of the analysed trait across species it is possible to infer its original state in a common ancestor (Haun, Jordan, Vallortigara, & Clayton, 2010). Recent studies in developmental psychology discovered a sensitivity to the mental states of others in early infancy (e.g., Onishi & Baillargeon, 2005), further strengthening the suggestion that the human ToM has an longstanding evolutionary basis. Because of their closed relatedness to humans as well as their highly complex social groups, great apes make up for an excellent model to shed light on the understanding of human socio-cognitive traits such as a ToM.

1.4 Great Ape Social Life

The great ape clade (*Hominidae*), besides humans (*Homo*), includes three extant genera: orangutans (*Pongo*) being the most distantly related to humans (divergence from the lineage of the other great apes around 14 Ma ago), followed by gorillas (*Gorilla*; speciation around 8 Ma ago) and the genus *Pan*, which encompasses the species bonobos, *P. paniscus*, and chimpanzees, *P. troglodytes*, with a speciation at around 6 Ma ago being most closely related to humans (Raaum, Sterner, Noviello, Stewart, & Disotell, 2005).

Orangutans, with the distribution areas of the two species *P. abelii* and *P. pygmaeus* being the islands Sumatra and Borneo respectively, are the only great apes living in Southeast-Asia. Further they are the most arboreal and solitary of all the great apes. Nevertheless, they maintain complex social networks and are considered to form individual based fission-fusion societies (van Schaik, 1999). Adult females and males lead a semi-solitary life within extensively overlapping home ranges of respectively around 8.5 and 25 km² size (Singleton & van Schaik, 2001). While mothers and their dependent offspring constitute the most frequent social associations, in times of food abundance, orangutans may come together in temporary feeding aggregations, travel bands and consortships (Sugardjito, te Boekhorst, & van Hooff, 1987). The orangutan mating system is highly promiscuous with males as well as females copulating with various individuals of the opposite sex. In spite of their solitary lifestyle orangutans are far from being antisocial and display a range of social behaviours (e.g., allogrooming, social play, communicative behaviours) when interacting with conspecifics.

There are two species of gorillas. The western gorilla, *G. gorilla*, with the main distribution area reaching from the Southern Central African Republic to the Congo River, the African west coast (*G. g. gorilla*) and the border region between Nigeria and Cameroon (*G. g. diehl*), and the eastern gorilla, *G. beringei*, who is found in the Virunga Volcanoes region, the Bwindi Impenetrable National Park in southwestern Uganda (*G. b. beringei*) and in the eastern Democratic Republic of Congo (*G. b. graueri*). Gorillas are the most terrestrial great apes. They have a polygynous mating system and usually live in cohesive social groups consisting of one adult male (silverback) monopolizing several females and their offspring (harem group). Both sexes disperse from their birth group. While females join other harem groups, males wander alone until they attract other females and build up a harem group of their own, or they associate with other males to form male-only bachelor groups. Groups vary in number from 2–30 individuals, home range sizes from 7–17 km² (Yamagiwa, Kahekwa, & Basabose, 2003). Within harem groups, females show markedly more friendly interactions with the silverback than with unrelated females (Harcourt & Stewart, 2007), and while unrelated females rarely interact at all, related females display a range of friendly social behaviours and support each other in conflicts (Stewart & Harcourt, 1987).

The genus *Pan* consists of the two species bonobos, *P. paniscus*, and chimpanzees, *P. troglodytes*, the lineages of which separated from each other about 2 Ma ago (Raaum et al., 2005). While bonobos are endemic in the Democratic Republic of Congo, chimpanzee populations are more widespread and can be found in West Africa (*P. t. verus*), Cameroon and Nigeria (*P. t. vellerosus*), Central Africa (*P. t. troglodytes*) and in the Congo Basin (*P. t. schweinfurthii*). Both species have a promiscuous mating system and form large fission-fusion communities of up to well over 100 individuals that regularly associate with another. The composition and size of temporary subgroups (parties) is highly variable and depends on food availability and the presence of estrous females (Anderson, Nordheim, Boesch, & Moermond, 2002; Hohmann & Fruth, 2002). Males remain in their natal community whereas females emigrate to neighbouring communities (male philopatry).

Chimpanzee communities are characterized by strong dominance hierarchies in which all adult males are dominant over females and high levels of inter- and intragroup aggression. Chimpanzees frequently engage in tool-assisted extractive foraging and sophisticated tool making. While chimpanzee females do not frequently interact with each other, males participate in coordinated hunts and border patrols to defend the territory against males from neighbouring communities. In contrast, bonobo females entertain close social associations with one another and are co-dominant to males (Surbeck, Deschner, Schubert, Weltring, & Hohmann, 2012). Bonobos are generally more peaceful and tolerant of each other than chimpanzees (Hare, Melis, Woods, Hastings, & Wrangham, 2007) and bonobo communities are overall more egalitarian (Furuichi, 1997). Bonobo sexual interactions serve also non-reproductive goals, such as the reduction of tension or as currency in social bartering (e.g., to obtain food). Because of the pronounced differences in social life and ecology bonobos and chimpanzees are often considered as separate species in studies investigating the cognitive skills of great apes; whereas the different species within the genera orangutan and gorilla are usually subsumed for analysis.

1.5 Great Ape Social Cognition

Since the seminal study of Premack and Woodruff (1978), many studies employing various paradigms in differing contexts have been conducted to investigate whether great apes share the human capacity of mind reading. Despite some conflicting results (e.g., Povinelli, Perilloux, Reaux, & Bierschwale, 1998), most of these studies suggest that great apes understand others' actions in terms of their underlying intentions. For instance, chimpanzees and orangutans have been found to discriminate between the accidental and the intentional placement of a marker indicating the location of food (Call & Tomasello, 1998). Likewise, in a helping paradigm, chimpanzees are more inclined to return an object if the human dropped it accidentally than when she threw it away intentionally (Warneken & Tomasello, 2006). Furthermore, chimpanzees are more patient (evidenced by longer waiting times and a lower frequency of gestural requests) when a human experimenter is unable to give food than when he is unwilling to do so (Call, Hare, Carpenter, & Tomasello, 2004). When copying others' failed actions, they reproduce the intended goals without observing the final sequence of the movement pattern or their outcome (Tomasello, Carpenter, Call, Behne, & Moll, 2005). 'Enculturated' chimpanzees (i.e., chimpanzees raised in very close contact to human caretakers) are also more likely to reproduce others actions if the action appears to be voluntarily executed instead of being the consequence of physical constraints, that is, they seem to rationally imitate (D. Buttelmann, Carpenter, Call, & Tomasello, 2007).

Great apes seem also to be capable of discriminating the human emotional expressions of happiness and disgust, and of exploiting them flexibly to attain hidden food (D. Buttelmann, Call, & Tomasello, 2009). In a task in which they had to choose between two containers with hidden food, all great apes preferentially chose the container to which the human reacted with happiness over the one to which the human reacted with disgust. However, they exhibited a reversed preference if they observed the human apparently eating one of the both food rewards (without knowing which one exactly) before making their choice. Overall, this might be indicative of an understanding of (some) desires in great apes.

Many studies have also investigated whether great apes understand others visual perceptions in terms of a mental state. At the most basic level all great apes have been found to geometrically follow the gaze of others to distant and out-of-sight targets. In doing so, they ignore distractors and move around barriers to match their own perspective to the one of others. Further they check back to the looker if they are unable to trace a gazing target. Overall, these results suggests that great apes understand the directed gaze of others as ‘seeing’ (reviewed in Rosati & Hare, 2009). Another set of studies probe great apes’ understanding of visual attention. In one of the first experimental tasks of this kind (Povinelli & Eddy, 1996b), chimpanzees had to choose between two human experimenters when begging for food. Whereas one of the experimenters could see the participants, the other could not (e.g., due to being oriented away, wearing a bucket, the eyes being occluded by a blindfold or being closed). The chimpanzees failed to spontaneously discriminate between the attentive and the inattentive experimenter in all conditions except for in the one in which they had to choose between an experimenter who was oriented towards them and an experimenter who was oriented away. However, more recent studies (Bania & Stromberg, 2013; Kaminski, Call, & Tomasello, 2004; Tempelmann, Kaminski, & Liebal, 2011) suggest that the chimpanzees’ performance in Povinelli and Eddy’s study might have been impeded by a confound of visual attention and body orientation (which also provided information about the experimenter’s disposition to hand the requested food). For instance, naturalistic observations of the communicative behaviour of captive great apes have shown that they direct their visual gestures predominantly to attentive recipients (chimpanzees: Liebal, Call, & Tomasello, 2004; orangutans: Liebal, Pika, & Tomasello, 2006; gorillas: Pika, Liebal, & Tomasello, 2003; bonobos: Pika, Liebal, & Tomasello, 2005). Likewise, they increase the frequency of their visual gestures if requesting food from an attentive recipient in comparison to a visually inattentive recipient (bonobos: Genty, Neumann, & Zuberbühler, 2015; chimpanzees: Hostetter, Russell, Freeman, & Hopkins, 2007; gorillas and orangutans: Poss, Kuhar, Stoinski, & Hopkins, 2006). Further, they first move into an recipient's line of sight before producing visual gestures if given the possibility to do so (Liebal, Pika, Call, & Tomasello, 2004). Overall, great apes' begging behaviour in food request paradigms seems to be heavily influenced by the recipient's body orientation, which is indicating visual attention as well as the disposition to give food. If these two factors are experimentally teased apart by delivering requested food via an apparatus such that the body orientation is irrespective of the disposition to give food, all great apes focus in their gestural communication on the recipient's eyes (Tempelmann et al., 2011).

While the studies mentioned above were investigating the understanding of visual attention in communicative contexts, a second line of research has established that great apes are also capable of using this understanding in competitive situations. In one such paradigm subordinate chimpanzees in the presence of a dominant individual had to choose between two contested pieces of food—one that was visible to both individuals and another one that was hidden from the dominant's sight and thus exclusively visible to the subordinate. Since subordinates got a head start when making a choice, there were no obvious behavioural cues from the dominant chimpanzee. Yet, the subordinates preferentially retrieved the piece of food that was hidden from the dominant's sight (Bräuer, Call, & Tomasello, 2007; Hare, Call, Agnetta, & Tomasello, 2000). Likewise, other tasks in which chimpanzees were required to retrieve food contested by a human competitor have demonstrated that chimpanzees preferentially approached the food via a route hidden from the competitor's sight (Hare, Call, & Tomasello, 2006) and preferentially chose to grasp food through a tunnel concealing their reaching from the competitor (Melis, Call, & Tomasello, 2006). In addition, there is also evidence that chimpanzees and bonobos keep track of what others have seen in the past (Hare, Call, & Tomasello, 2001; Kaminski, Call, & Tomasello, 2008; MacLean & Hare, 2012).

While it seems clear that apes understand what others can and cannot see (level-1 perspective-taking), evidence for an understanding of *how* others perceive objects from their perspective (level-2 perspective-taking) is far more ambiguous. For instance, Karg, Schmelz, Call, and Tomasello (2015) found that chimpanzees in a competitive foraging task were more likely to retrieve food from a box that was covered with a screen that was opaque than from a box covered with a screen that appeared to be opaque from the participant's perspective but was in fact transparent from the competitor's viewing angle. In another competitive foraging task chimpanzees had to choose between food sticks that had the same size but were attached to a screen in such a way that one appeared to be longer from the conspecific competitor's point of view (Karg, Schmelz, Call, & Tomasello, 2016). After the competitor made a choice in private, the chimpanzee participants preferentially retrieved the stick that appeared to be shorter from the competitor's perspective, while exhibiting the reversed preference in a nonsocial control. However, their performance broke down to chance level when the screen and the sticks were rearranged such that the participants themselves had no more preference for either stick. Thus, instead of human-like level-2 perspective-taking, chimpanzees rather engage in projection of self-preference and self-experience to understand how others perceive objects (Karg et al., 2016). In line with this interpretation, other studies with the same basic competitive foraging paradigm also indicate that chimpanzees might use their own preference to predict the competitor's choice (Schmelz, Call, & Tomasello, 2011, 2013).

While great apes show a profound and flexible understanding of others' visual perceptions, evidence for an understanding of others' beliefs is scarce. Although a recent study demonstrated that great apes—like human infants—exhibit an implicit sensitivity to others' false beliefs (Krupenye, Kano, Hirata, Call, & Tomasello, 2016), to date they have failed in all studies that required an explicit understanding of others' false beliefs (Call & Tomasello, 1999; Kaminski et al., 2008; Krachun, Carpenter, Call, & Tomasello, 2009, 2010; O'Connell & Dunbar, 2003). This might be due to the cognitive demands of handling multiple conflicting perspectives, with their own knowledge of reality being dominant ('pull of reality'; e.g., Keysar, Barr, Balin, & Brauner, 2000; Mitchell, Robinson, Isaacs, & Nye, 1996). This kind of egocentric interference even affects human adults who are proficient mind readers (Apperly et al., 2010; Apperly, Samson, & Humphreys, 2009; Birch & Bloom, 2007). Moreover, developmental studies have demonstrated that ToM development in infants correlates with their proficiency in tasks relating to executive function (Qureshi et al., 2010; Rakoczy, 2010; Sabbagh et al., 2006), presumably due to inhibitory control allowing individuals to suppress their own perspective.

An important caveat in regards to what has been discovered about great ape mind reading skills is that many studies have only investigated chimpanzees' performance. However—as argued before—to delineate the evolution of a human cognitive capacity like ToM it is crucial to understand the mind reading skills of all the great apes.

1.6 Focus of the Current Dissertation

In my dissertation, I will attempt to contribute to a more complete understanding of great ape mind reading. In particular, I am testing hypotheses about the evolutionary origins of different aspects of perspective-taking and false belief understanding by exploring and comparing different great ape species who stem from different social environments, including bonobos (study 2), chimpanzees (study 2 and 3), gorillas (study 2), orangutans (study 1 and 2), as well as human infants and children (study 2 and 3). To account for the distinctive social environments that these species are stemming from, and to test how flexibly they use their socio-cognitive skills, I conducted the studies in competitive situations (study 1 and 3) and a communicative cooperative paradigm (study 2). In addition to insights into the respective great apes' mind reading skills, it is anticipated that the comparative approach (across species and living contexts) will develop understanding about selective pressures which were most relevant in shaping great ape social intelligence.

The purpose of study 1 was to extend what is known about orangutans' level-1 perspective-taking skills to the competitive domain. Adopting the paradigm of a study conducted with chimpanzees (Melis et al., 2006), I examined whether orangutans, like chimpanzees, would adjust their behaviour in a way that prevents a human competitor from seeing them steal a piece of food. In the task, participants were required to reach through one of two opposing plexiglass tunnels in order to retrieve a food reward. Both rewards were also physically accessible to a human competitor sitting opposite the participant. Participants always had the possibility to reach one piece of food outside the human's line of sight. This was because either the human was oriented to one but not the other reward (while both tunnels were transparent) or because one tunnel was covered by an opaque barrier and the other one remained transparent (while the competitor was facing both rewards). Because orangutans are most distantly related to humans, and competitiveness is less pronounced in orangutans than in chimpanzee societies, it is unclear whether they are able to use their understanding of what others can see in a competitive context. If they were able to succeed in the task this would indicate an early evolutionary emergence of a flexible understanding of visual attention in the great ape clade.

The aim of study 2 was to gain insight whether great apes' conceptualization of visual attention goes beyond the understanding of a mental state which can merely be either present or absent. More specifically, I wanted to explore whether great apes recognize others' attention towards an external referent can be altered by communicative means. To investigate such communicative strategies I compared the communicative behaviours of all four great ape species and 20 month old human infants who requested rewards from a human experimenter. If great apes point to direct a recipient's attention towards an out-of-sight referent, this would suggest that their gestural communication is going beyond the achievement of material goals and demonstrate a genuine intention to change others mental states through providing information. Ultimately, positive results would provide support for a cognitively rich interpretation of great ape gestural communication.

In study 3, I conducted research on chimpanzees' understanding of others false beliefs. Recent studies have demonstrated that young infants are sensitive to others' belief states long before they pass explicit false belief tasks (reviewed in Baillargeon, Scott, & He, 2010). Similarly a very recent study demonstrated false belief sensitivity in great apes (Krupenye et al., 2016). Some have argued that infants' lack of inhibitory control might be responsible for their failure in latter tasks. Likewise, a lack of inhibitory control might have been precluding chimpanzees' implicit capacities to compute others' beliefs in all studies to date. Therefore, my goal in study 3 was to devise a false belief task with reduced requirements for executive function. To this end, I employed the basic paradigm from Kaminski et al. (2008) in which chimpanzees competed in a turn-taking game with a conspecific for hidden reward. I modified the paradigm by ensuring (1) participants did not have any preference amongst the alternative choices ('no preference' task) or (2) they did not have any knowledge of the location of the preferred reward ('no knowledge' task). To be better able to relate the results to human false belief understanding, 5.5 year old preschool children were tested in the same paradigms as the chimpanzees. If chimpanzees should succeed in the task this would further strengthen the argument for an evolutionary ancient, and early developing, core mechanism of belief understanding in humans (e.g., Leslie, Friedman, & German, 2004). Additionally this would imply that this core mechanism was already present in the last common ancestor of the genera *Pan* and *Homo*. In contrast, negative results would be in accordance with results from previous studies where chimpanzees failed to demonstrate any explicit understanding of others' (false) beliefs; suggesting that this capacity specifically evolved in the human lineage.

2. Study 1

Orangutans in a Competitive Perspective-Taking Task

Adopting the paradigm of a study conducted with chimpanzees, *Pan troglodytes* (Melis et al., 2006), I investigated orangutans', *Pongo pygmaeus*, understanding of others' visual perspectives. More specifically, I examined whether orangutans would adjust their behaviour in a way that prevents a human competitor from seeing them steal a piece of food. In the task, participants had to reach through one of two opposing plexiglass tunnels in order to retrieve a food reward. Both rewards were also physically accessible to a human competitor sitting opposite the participant. Participants always had the possibility of reaching one piece of food that was outside the human's line of sight. This was because either the human was oriented to one, but not the other, reward or because one tunnel was covered by an opaque barrier and the other remained transparent. In the situation in which the human was oriented towards one reward, the orangutans successfully avoided the tunnel that the competitor was facing. If the human was oriented towards both rewards, but one tunnel was covered, they reached the food marginally more often through the opaque versus the transparent tunnel. However, they did so by frequently first inspecting the transparent tunnel (then switching to the opaque one). Considering the participants' initial inspections, they chose randomly between the opaque and transparent tunnel, indicating that their final 'reach decision' was probably driven by a more egocentric behavioural rule. Overall, the results suggest that orangutans have a limited understanding of others' perspectives, relying mainly on cues from facial and bodily orientation, as well as egocentric rules, when making such judgements.

2.1 Introduction

The capacity to take the visual perspective of others is an integral part of human social interactions, especially when it comes to judging whether, and how, others will perceive and react to events in their environment. Whereas human children excel in visual perspective-taking from early on (Flavell, Everett, Croft, & Flavell, 1981; Moll & Meltzoff, 2011a), as of yet it remains unclear to what extent this trait is uniquely human or shared with other animal species. The ability to follow the gaze of others, which is thought of as a prerequisite for more sophisticated forms of understanding what others 'see', seems to be widespread in the animal kingdom (primates: Call, Hare, & Tomasello, 2001; ungulates: Kaminski, Riedel, Call, & Tomasello, 2005; birds: Loretto, Schloegl, & Bugnyar, 2010; reptiles: Wilkinson, Mandl, Bugnyar, & Huber, 2010). However, evidence for higher-level gaze following that is not explicable in terms of a simple co-orientation response (Povinelli & Eddy, 1996a) is scarcer. So far only wolves, *Canis lupus* (Range & Virányi, 2011), ravens, *Corvus corax* (Bugnyar, Stöwe, & Heinrich, 2004) and some primates (Amici, Aureli, Visalberghi, & Call, 2009; Bräuer, Call, & Tomasello, 2005) have been found to follow the gaze of others behind barriers, while only primates are reported to visually check back with the looker if being unable to trace a potential target in their sight (primate gaze following reviewed in Rosati & Hare, 2009).

Furthermore, there are two major lines of evidence indicating that several species are able to track the attentional state of others. One line of support comes from investigations of communicative interactions. For instance, dogs, *Canis familiaris* (Gácsi, Miklósi, Varga, Topál, & Csányi, 2004), dolphins, *Tursiops truncates* (Xitco, Gory, & Kuczaj, 2004), horses, *Equus caballus* (Proops & McComb, 2010), multiple primate species (Hattori, Kuroshima, & Fujita, 2010; Kaminski et al., 2004; Liebal, Pika, & Tomasello, 2004; Povinelli & Eddy, 1996a; Tempelmann et al., 2011), and birds such as ravens (Pika & Bugnyar, 2011) are known to address their begging behaviour and visual gestures predominantly to attentive recipients. There is also some evidence that chimpanzees, *Pan troglodytes*, vocalize more frequently when requesting food from an inattentive human, possibly as a strategy to draw the human's attention to themselves (Hostetter, Cantero, & Hopkins, 2001; Hostetter et al., 2007; Leavens, Russell, & Hopkins, 2010).

A second line of evidence stems from investigations of competitive situations. As recently demonstrated, food competition paradigms seem to be ecologically more valid to many animal species and thus more likely to elicit complex cognitive abilities (Hare, 2001). Various animals tested in such situations take into account the attentional focus of conspecifics and humans and avoid food that is visible to their competitor (i.e., depending on the paradigm, either being more reluctant to retrieve such food or, instead, preferring alternative food invisible to their competitor). These types of strategic behaviours are evidenced in species as distantly related as dogs (Bräuer, Call, & Tomasello, 2004; Call, Bräuer, Kaminski, & Tomasello, 2003), goats, *Capra hircus* (Kaminski, Call, & Tomasello, 2006), jackdaws, *Coloeus monedula* (von Bayern & Emery, 2009), scrub-jays, *Aphelocoma coerulescens* (Emery & Clayton, 2001), starlings, *Sturnus vulgaris* (Carter, Lyons, Cole, & Goldsmith, 2008), and several primates (Bräuer et al., 2007; Burkart & Heschl, 2007; Flombaum & Santos, 2005; Sandel, MacLean, & Hare, 2011). However, it remains unclear whether the participants in these tasks really consider what the competitor can 'see'. As the competitor might appear to be absent when individuals move behind a barrier (or overt cues such as visibility of the eyes and eye aversion differed between conditions), the participants' choice may in fact be egocentrically based. Moreover, chimpanzees and corvids apparently not only understand what another individual can see in the present but also what others have seen in the past (Bugnyar, 2011; Bugnyar & Heinrich, 2005; Dally, Emery, & Clayton, 2006; Hare et al., 2001; Kaminski et al., 2008).

Finally, some animals also actively conceal visual information from competitors (Dally, Emery, & Clayton, 2004; Hare et al., 2006; Melis et al., 2006). For instance, Dally et al. (2004) found that scrub-jays who were observed by potential pilferers preferred to cache food in a tray (viewable by the pilferers) that was positioned in the shade over one more exposed to light, and exhibited no such cashing preference if it was carried out in private (i.e., out of sight of pilferers). Notably, pilferers were equally well visible from both trays, ruling out the idea that the scrub-jays were using immediate perceptual cues to solve the task. Similarly Hare et al. (2006) reported chimpanzees to actively conceal the theft of contested food from the view of a human competitor. In the critical experimental conditions of this study, the two food pieces that the chimpanzees could choose from were either positioned such that the human could see both or none. However, one approach route provided cover from the competitor's view while the second one did not. In one condition this was because the competitor's face was oriented towards one side but not the other. In a second condition participants could approach from behind either a transparent barrier or an opaque occluder. In the third condition one side was obstructed by a barrier that fully shielded their approach while the other side was occluded by a (split) barrier that only partially shielded their approach (allowing the human to see the lower body parts of the approaching chimpanzee). In all conditions the chimpanzees consistently chose to approach the contested food via the hidden route (whereas they did not when no competitor was present). Although the chimpanzees could not succeed in the latter two conditions by merely avoiding the route that the competitor was looking at, nevertheless it could be the case that they were simply avoiding the side that allowed them to see the human's face or body parts. To rule this possibility out, Melis et al. (2006) conducted a study in which both pieces of food were visible to the competitor while each of the approaching paths leading to the food was completely out of her view. Hence, the competitor was entirely hidden from the chimpanzees when they were trying to retrieve the reward. However, the competitor could potentially see their attempt to steal the food, depending on whether they chose to reach through a clear or opaque tunnel. Thus, the chimpanzees had to 'imagine' what the competitor could see from her perspective. Similarly, as in the study of Hare et al. (2006), the chimpanzees preferentially chose to reach through the opaque tunnel.

In summary, it seems that although many animals show some basic sensitivity to what others see (either indicated by their ability to follow the gaze of others or taking into account the attentional state of others), as of yet the most conclusive evidence for perspective-taking-like capacities comes from experiments with corvids and great apes. However, this might be the result of a focus of research on relatively few species. This discrepancy precludes us from drawing firm conclusions about the evolutionary trajectory of this capacity. For instance, most of the evidence for great apes' perspective taking stems from studies with chimpanzees, whereas much less is known about the other great ape species. As chimpanzees (along with bonobos, *Pan paniscus*) are the closest relatives to humans, and because they also live in highly complex social groups, their perspective-taking skills might be unique (or at least be most profound) among great apes. However, the trait might be evolutionarily more ancient and therefore also present in the other great ape genera. As orangutans, *Pongo pygmaeus*, are phylogenetically the most distant of all great apes from humans, as well as the least sociable anthropoid primate species, they represent the ideal test case to resolve this issue.

Orangutans are the most arboreal great ape species. Their lineage split from that of the other great apes 12–16 million years ago (Locke et al., 2011). Orangutan life history is characterized by a long life span (35–45 years in the wild, more than 55 years in captivity), slow development and long interbirth intervals (with 8 years the longest among mammals), which might be linked to prolonged learning (Delgado & van Schaik, 2000). Indeed, evidence from the wild indicates that orangutan behaviour and tool use are to some extent socially transmitted (Krützen, Willems, & van Schaik, 2011; van Schaik et al., 2003). Apart from mothers and their dependent offspring, orangutans spend most of their time alone. However, during periods of high food abundance they sometimes form small feeding aggregations as well as travel bands (Sugardjito et al., 1987; te Boekhorst, Schürmann, & Sugardjito, 1990). Therefore, orangutan social structure is thought of as an individual-based fission fusion system (van Schaik, 1999).

As yet, evidence for perspective-taking in orangutans is sparse. In following the gaze of others around barriers, orangutans seem to be less sensitive to the features of objects obstructing the gazer's line of sight than the African great ape species are (Okamoto-Barth, Call, & Tomasello, 2007). When requesting food from a human experimenter who had the food in front of her but was orientated away from the participant, the orangutan reliably moved into the experimenter's line of sight (Liebal, Pika, Call, et al., 2004). If the location of the food did not correspond with the experimenter's body orientation, orangutans (unlike chimpanzees and bonobos) occasionally either stayed where they were or manoeuvred behind her and frequently gestured even though the experimenter was unable to see them. By contrast, Shillito, Shumaker, Gallup, and Beck (2005) reported that a single female was highly sensitive to the visual states of humans who she directed to desirable objects beyond her reach. Furthermore, orangutans 'point' more frequently to the location of a hidden tool, if the helper needing the tool to retrieve food for them is ignorant of its whereabouts (Zimmermann, Zemke, Call, & Gómez, 2009). In summary, the existing results are inconsistent, and no study to date has explored orangutans' understanding of others' visual perspectives in a competitive context.

By adopting the paradigm of Melis et al. (2006) for the present study, my goal was to close this gap, thereby providing more comparative data to trace the evolutionary history of (human) perspective-taking. In this task, participants retrieved one of two pieces of food, both of them positioned in front of two opposing plexiglass tunnels. Although participants could approach either reward unseen, only one reward could be reached without the human seeing. In one condition this was because the human was oriented to one but not the other reward. In a second condition the competitor faced both rewards, but one of the two tunnels was covered by an opaque barrier, shielding the orangutans' grasp from the human's view.

2.2 Methods

Participants. The participants were 13 Bornean orangutans (eight females and five males; see Appendix A.1) housed at the Orangutan Care Centre and Quarantine in Pasir Panjang, Kalimantan Tengah, Indonesia. The orangutans' ages ranged from 7.5–12.0 years (average age 8.9 ± 1.3 years). All of them were born in the wild and came to the sanctuary after being rescued at an early age (range 0.5–4.0 years; average age 1.6 ± 1.1 years) as a result of the logging of rainforest and the trade of orangutans for pets. Once the apes arrived at the sanctuary, they were raised by human caretakers together with peers until they were old enough to join a social group with mates of their respective sex of roughly the same age. During the night, the groups were housed in indoor enclosures. During the day, the orangutans were regularly allowed to forage in a nearby area of tropical forest. The orangutans were fed various fruits, vegetables and cereals three times a day and were not food deprived for testing at any time. Water was available ad libitum.

Experimental set-up. Participants were tested individually in a testing area consisting of five connected cages (each with a base area of 1.5 x1.5 m) that were arranged in a U-shaped manner, forming a testing booth (see Fig. 1). Two holes (10 x 5 cm) in the centre of the cages at the end of each arm of the U (henceforth 'target cages') led to the inner booth area. Plexiglass tunnels (25 x 25 cm and 21 cm high) were fixed to the booth side of the cagewalls in front of the holes. A plexiglass flap was fixed inside each tunnel 24 cm away from the hole. The flaps had to be pulled open to reach a food reward placed on a wooden platform (25 x10 cm) that was attached in front of each of the tunnels. The experimenter (E) sat on a wooden box positioned 1.2 m away from the middle cage, centred within the booth and between both plexiglass tunnels. A small plastic bin (8 x 5 cm and 5 cm high) was fixed to the mesh of the middle cage. Between trials E smeared a food reward (e.g., honey) on the bin to attract participants to the frontal middle of the central cage (from where they were able to see E as well as the plexiglass tunnels and both rewards).

During warm-up trials, the wire mesh walls surrounding the tunnels of the target cages were covered with wooden plates, whereas the wire mesh of the central cage remained uncovered. For the actual experiment additional visual barriers were added to the general set-up. All three cage walls facing the booth were entirely covered with wooden boards, occluding the approaching paths to both target cages. The only openings that remained uncovered were the two holes leading to the interior of the tunnels and a narrow gap in the middle of the central cage (width 17 cm, height 60 cm, starting 25 cm above the cage floor). The latter allowed the orangutans to feed from the bait bin and to observe the complete set-up within the booth. To make it more difficult for the orangutans to spot E (or parts of E's body) through the tunnel openings, stripes of opaque adhesive tape (creating a band 10 cm wide) were stuck to the tunnel walls over the cage holes.

General Procedure. The general procedure for warm-up and experimental trials was as follows. While participants were feeding from the bait (e.g., the honey), E placed a reward (e.g., a peanut) in front of each of the tunnels. Then he sat down opposite the participant in a position dictated by the experimental condition (see below). A trial started after participants had finished eating the bait and left their central (starting) position. To reach the food, participants had to approach either of the two target cages and pull open the flap door of the respective tunnel. If they opened the flap door in view of E, E immediately retracted both food rewards and banged on the opened tunnel with a small wooden stick (to further emphasize the competitive nature of the task). If the participants approached and pulled open the flap of the tunnel that was out of E's line of sight, they were allowed to retrieve the reward. A trial ended either when the participants retrieved the food or after 90 s had passed without the participant opening either of the tunnels.

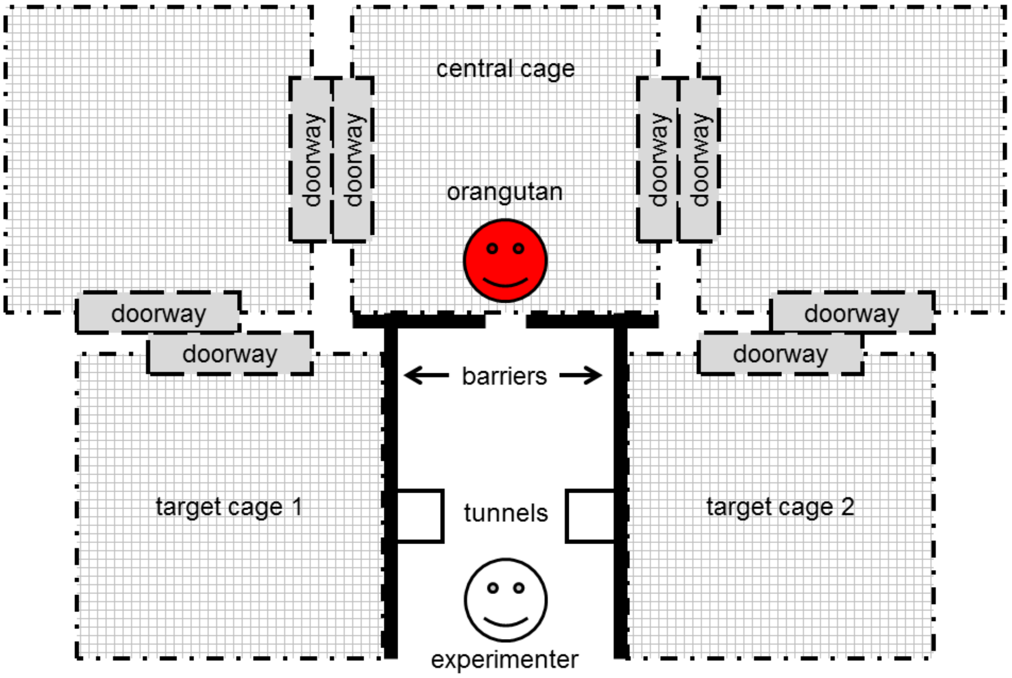

Figure 1. Experimental setup

Warm-up trials. Before testing, all participants were familiarized with the general set-up and the competitive nature of the task in a series of warm-up trials. In the warm-up trials, E turned his head and body towards either of the respective sides, looking at one of the tunnels. If the participants opened the flap door in front of E, E withdrew both food rewards before the participants could reach it. If the participants pulled open the flap of the tunnel at E's back, they were allowed to retrieve the reward. Only participants who had successfully retrieved four rewards in a row (within a maximum of 36 trials, split into two sessions on consecutive days) were chosen to participate in the study (see Appendix A.1).

Experimental trials. For the actual experiment additional visual barriers were added, so that the approaching paths to both tunnels were completely occluded. During testing participants experienced three different conditions in a within-subject design (see Fig. 2):

Body orientation condition (BO). As in warm-up trials, both tunnels remained transparent and E was oriented towards one but not the other reward.

Hidden-visible condition (HV). E sat facing the central cage, holding the stick in both hands while looking straight ahead (but never establishing direct eye contact with the participant). One of the tunnels was opaque (covered by a blue plastic sheath) and the other remained transparent.

Nonsocial control (NS). To investigate whether the orangutans had a general preference for one of the tunnels, I conducted a control condition identical to the hidden-visible condition except that E left the testing area after placing the food rewards in front of the tunnels. Trials ended with E returning after 90 s or when both rewards had been retrieved.

Participants received a total of 54 trials (18 per condition) split up in two daily sessions of nine-trial-triplets. Sessions were presented on consecutive days. Each triplet was composed of one trial per condition. Owing to lack of motivation, with one participant (Imas) the second daily session had to be interrupted for a number of hours, and with two others (Kraba, Cabang) the trials had to be split up into three daily sessions. The location of the opaque (and the transparent) tunnel was counterbalanced such that in half of the trials the opaque tunnel was on the left while in the other half it was on the right. The location of the opaque tunnel was also semi-randomized such that the reward could not be retrieved on the same side in more than two consecutive trials. The same was true for the orientation of E in the body orientation condition.

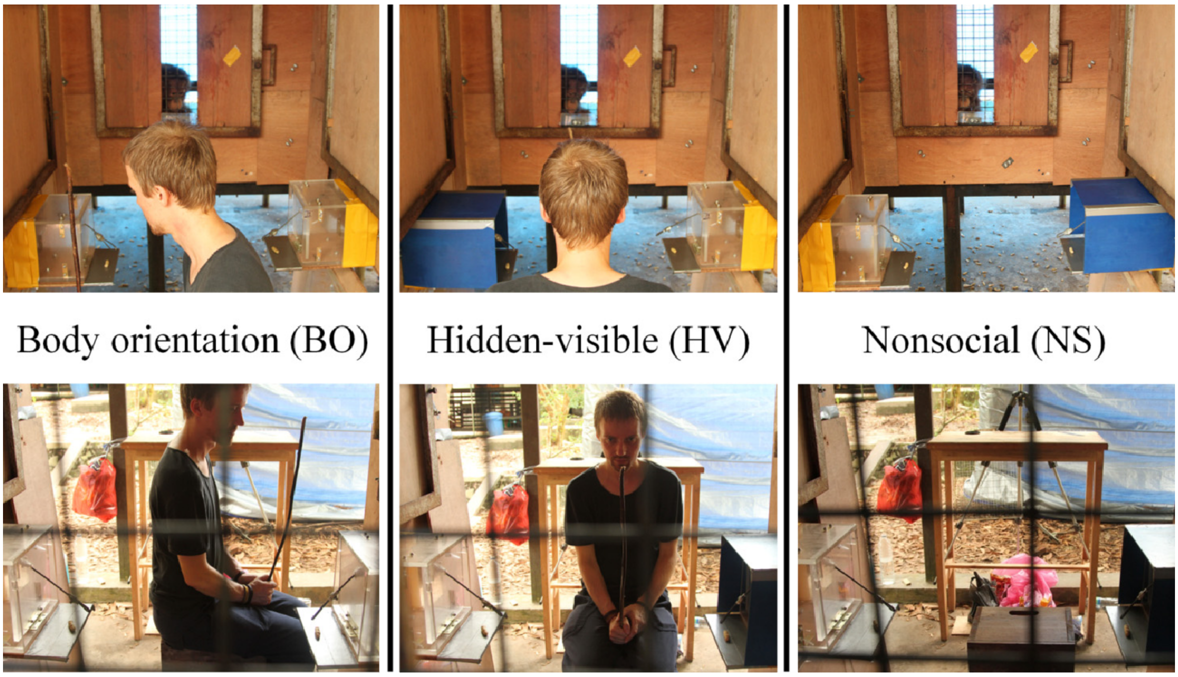

Figure 2. Experimental conditions; upper row: booth side view; lower row: ape side view

Coding and analysis. All trials were recorded by three digital camcorders from different angles and subsequently scored from the video files. I coded which tunnel the participants chose to retrieve the (first) reward. A ‘choice’ was defined as pulling open the flap door of the respective tunnel. I also coded which sides participants inspected before making their choice (or running out of time). An ‘inspection’ was scored when participants either looked through a tunnel opening or reached through the opening, as far as their wrists. I differentiated between two different types of inspections. The first tunnel participants chose to inspect was coded as ‘initial inspection’. If they inspected a tunnel and then approached and inspected the tunnel on the opposite side, the (latter) inspection was coded as a ‘side switch’. Finally, I coded how much time participants spent in total with the ‘initial inspection’. The total time was calculated by adding the duration of all single inspection events (i.e., looks and reaches), starting with the first inspection of one tunnel and ending with the pulling open of the tunnel's door flap or switching to the opposite tunnel. A second observer scored 20% of the trials to assess the inter-observer reliability of performance. Inter-observer reliability for participant's choice, initial inspections and side switches was excellent (Cohen's $\kappa = .99$, $\kappa = 1$ and $\kappa = .99$, respectively). The Spearman's correlation coefficient for the inter-observer reliability of initial inspection times was $\rho = .64$ ($p < .001$).

First, I compared the total number of trials in which participants refrained from opening any tunnel across conditions, plus, for each condition separately, whether participants were more likely to refuse to open the tunnel if (last) inspecting the in-view or out-of-sight tunnel. For participants' choice and initial inspections, I compared their preference for the out-of-sight tunnel across conditions as well as against chance. As participants did not make a choice or inspect any tunnel in some trials, the respective results were analysed using proportions. For side switches I compared the total number of trials in which participants switched sides (at least once) across conditions; plus, for each condition separately, whether participants were more likely to switch sides depending on the tunnel they had initially inspected. For initial inspection times, I compared the mean times across as well as within conditions. Moreover, I compared whether inspection times differed depending on which tunnel the participants inspected. For all behavioural measurements, I additionally compared participants' performance in the first nine trials with that in the last nine trials to check for learning effects. Because the data did not satisfy the criteria of normality of distribution and homogeneity of variance (based on Shapiro-Wilk and Levene's test), and as generalized linear mixed models have clear issues regarding the reliability of the *p* values (Bolker et al., 2009), I chose nonparametric Wilcoxon and Friedman tests as the most simple and reliable. Owing to the small number of participants, exact probabilities were calculated for all Wilcoxon tests. Unless otherwise stated, all reported *p* values are two-tailed.

2.3 Results

Participants' choice. A first look at the (absolute) number of trials in which participants refrained from making a choice (see Table 1) indicated a difference between conditions (Friedman test: $\chi^2 = 10.89$, $N = 13$, $p = .004$). Post hoc tests revealed that participants refused to choose most frequently in the HV condition (Wilcoxon signed-ranks test: HV–BO: $T_+ = 33.5$, $N = 8$, $p = .039$; HV–NS: $T_+ = 28.0$, $N = 7$, $p = .016$). The NS and the BO condition did not differ from each other ($T_+ = 10.0$, $N = 4$, $p = .125$). In the HV condition, participants were more likely to refuse to choose after (last) inspecting the transparent tunnel ($T_+ = 26.0$, $N = 7$, $p = .047$). In the BO condition, participants' reluctance to make a choice did not differ depending on whether they (last) inspected the in-sight or out-of-sight tunnel ($T_+ = 1.0$, $N = 1$, $p = 1$). The number of trials without any choice did not differ between the first and last nine trials of any condition (BO: $T_+ = 8.5$, $N = 4$, $p = .375$; HV: $T_+ = 16.0$, $N = 7$, $p = .781$).

Focusing on trials in which participants made a choice, I found that in the BO condition, orangutans preferentially chose the tunnel at E's back (Wilcoxon signed-ranks test against 50%; $T_+ = 73.0$, $N = 12$, $p = .005$; see Fig. 3). In the HV condition they chose the opaque tunnel marginally more (Wilcoxon signed-ranks test against 50%; $T_+ = 62.0$, $N = 12$, $p = .074$, and if one-tailed statistics are applied, as in Melis et al. 2006, this comparison reaches significance ($p = .037$)). In the NS control, participants showed no preference for either tunnel (Wilcoxon signed-ranks test against 50%; $T_+ = 38.5$, $N = 11$, $p = .659$). I then directly compared participants' preference for the tunnel at E's back in the BO condition and their preference for the opaque tunnel in the HV and NS conditions. This comparison revealed no significant differences (Friedman test; $\chi^2 = 2.52$, $N = 13$, $p = .284$). A comparison of the orangutans' preference in the first nine trials with their preference in the last nine trials did not reveal any significant changes for any of the conditions (Wilcoxon signed-ranks test; BO: T_+

= 32.0, $N = 10$, $p = .676$; HV: $T_+ = 52.0$, $N = 11$, $p = .098$; NS: $T_+ = 37.5$, $N = 10$, $p = .336$).

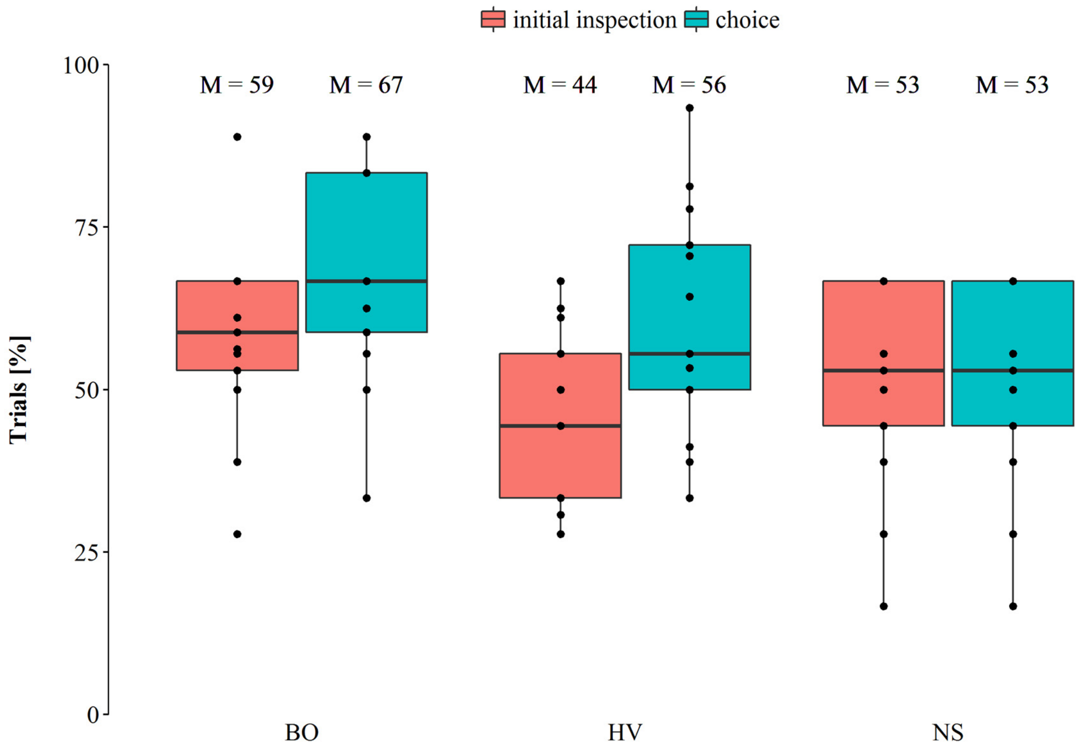

Figure 3. Box plot of % trials in which the orangutans initially inspected (red) and chose (blue) the out-of-sight tunnel. The middle lines represent population median values (denoted as M above each box); lower and upper hinges display first and third quartiles, respectively; whiskers extend up to 1.5 x interquartile range. Filled black circles represent individual data points. BO: body orientation condition; HV: hidden-visible condition; NS: nonsocial control.

Side switches. When E was present (i.e., in BO and HV), the orangutans sometimes switched sides before making their choice (see Table 1). This behaviour might have either been caused by a general feeling of insecurity in the presence of E or it occurred because the orangutans were deliberately changing their initial choice. In the former case the orangutans should switch sides equally often in both ‘social’ conditions and irrespective of which tunnel they were initially inspecting. To rule out one or the other explanation, I therefore analysed the frequency of side switches across conditions as well as between both tunnels. Comparing the number of trials with at least one side switch, I found a significant difference between conditions (Friedman test; $\chi^2 = 15.62$, $N = 13$, $p < .001$). Post hoc comparisons revealed that side switches occurred most frequently in the HV condition compared to the other conditions (Wilcoxon signed-ranks test; HV–BO: $T_+ = 43.0$, $N = 9$, $p = .016$; HV–NS: $T_+ = 55.0$, $N = 10$, $p = .002$). Side switches were also more frequent in the BO condition than in the NS control ($T_+ = 28.0$, $N = 7$, $p = .016$). Furthermore, the participants switched sides depending on which tunnel they initially inspected. In the BO condition participants were more likely to switch sides after initially inspecting the tunnel in front of E rather than after initially inspecting the tunnel behind his back ($T_+ = 28.0$, $N = 7$, $p = .016$). Likewise, participants in the HV condition were more likely to switch sides after initially inspecting the transparent tunnel rather than after initially inspecting the opaque tunnel ($T_+ = 50.5$, $N = 10$, $p = .016$). The frequency of side switches did not differ between the first and last nine trials of any condition (BO: $T_+ = 10.5$, $N = 6$, $p = 1$; HV: $T_+ = 29.0$, $N = 9$, $p = .516$).

Initial inspections. If the orangutans truly understood something about the competitor's perspective, the cues that were accessible from the starting position should have been sufficient for them to make a correct choice without first having to inspect any of the tunnels. Also, it might have been that some participants initially inspected the correct tunnel but refrained from retrieving the reward because they were scared by the competitor's presence. Therefore, I additionally analysed whether the orangutans had a tunnel preference when initially inspecting a particular side. In the BO condition, the orangutans initially inspected the tunnel at E's back marginally more often than expected by chance (Wilcoxon signed-ranks test against 50%; $T_+ = 62.5$, $N = 12$, $p = .067$; see Fig. 3). Participants did not show a preference in initially inspecting the opaque or the transparent tunnel, either in the HV condition (Wilcoxon signed-ranks test against 50%; $T_+ = 52.0$, $N = 12$, $p = .327$) or in the NS control (Wilcoxon signed-ranks test against 50%; $T_+ = 38.5$, $N = 11$, $p = .659$). Comparing a participant's preference to initially inspect the tunnel at E's back in the BO condition, with the preference to initially inspect the opaque tunnel in the HV and NS conditions, revealed no significant differences (Friedman test; $\chi^2 = 2.571$, $N = 13$, $p = .277$). Neither did I find any significant differences between the orangutans' performance in the first nine trials and their performance in the last nine trials (Wilcoxon signed-ranks test; BO: $T_+ = 39.0$, $N = 11$, $p = .633$; HV: $T_+ = 18.0$, $N = 6$, $p = .156$; NS: $T_+ = 37.5$, $N = 10$, $p = .336$).

Table 1.

Number of Trials Without Any Choice and With Side Switches

	No choice			Side switches		
Name	BO	HV	NS	BO	HV	NS
Ari	0	0	0	0	1	0
Cabang	1	9	0	1	3	0
Claire	0	1	0	1	1	0
Edwin	1	0	0	0	2	0
Galih	0	0	0	1	2	0
Imas	0	3	0	6	8	0
Kraba	2	4	0	1	0	0
Lanang	0	2	0	0	9	0
Mercedes	2	3	0	1	1	0
Noni	0	0	0	0	0	0
Osborne	0	0	0	3	5	0
Rowland	0	1	0	0	4	0
Sallie	0	0	0	0	0	0
Mean	0.5	1.8	0.0	1.2	3.0	0.0

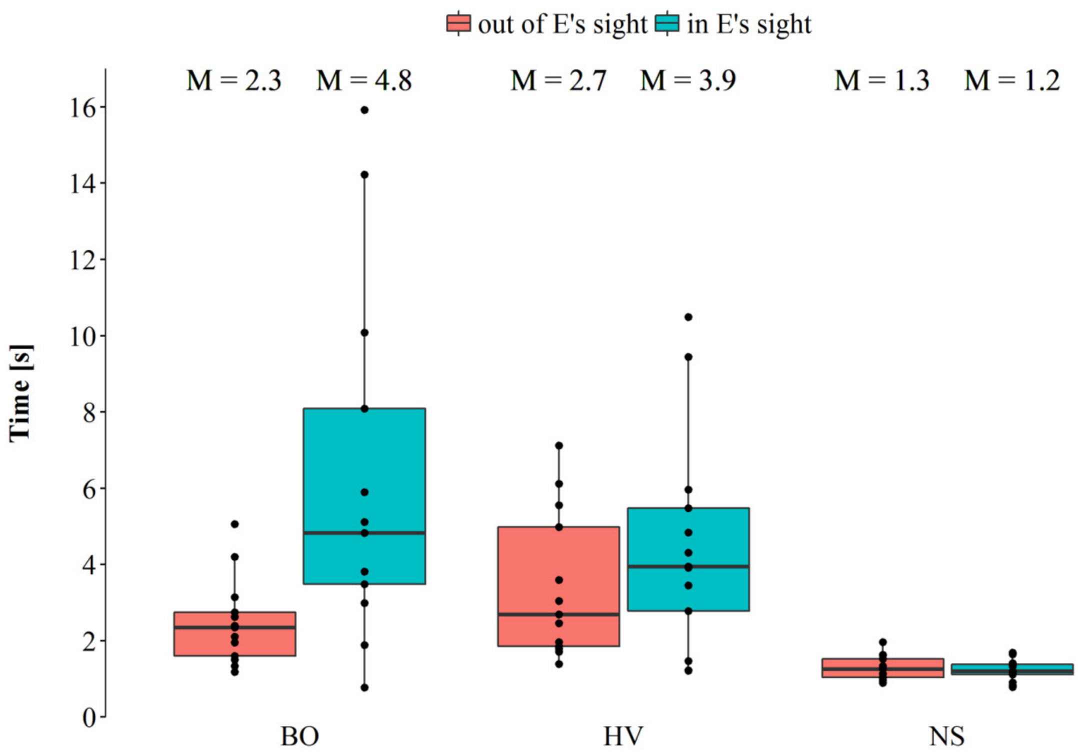

Figure 4. Box plot of the total duration that participants spent inspecting the out-of-sight tunnel (red) and the in-sight tunnel (blue). The middle lines represent population median values (denoted as M above each box); lower and upper hinges display first and third quartiles, respectively; whiskers extend up to 1.5 x interquartile range. Filled black circles represent individual data points. BO: body orientation condition; HV: hidden-visible condition; NS: nonsocial control.

Total time of initial inspections. Focusing on trials where participants made a choice without switching sides, I analysed how much time participants spent with the initial inspection of the tunnel. There was a significant difference between conditions (Friedman test; $\chi^2 = 16.77$, $N = 13$, $p < .001$, see Fig. 4). Post hoc comparisons revealed that initial inspection times were shortest in the NS control compared to the other conditions (Wilcoxon signed-ranks test; BO: $T_+ = 90.0$, $N = 13$, $p < .001$; HV: $T_+ = 91.0$, $N = 13$, $p < .001$). Mean initial inspection times did not differ significantly between the BO condition and the HV condition ($T_+ = 49.0$, $N = 13$, $p = .839$). Next, I analysed whether initial inspection times differed depending on which tunnel was inspected. In the BO condition, participants spent more time inspecting the tunnel in front of E than inspecting the tunnel at E’s back ($T_+ = 88.0$,

$N = 13$, $p = .001$). There was no significant difference between the time participants spent inspecting the transparent and the opaque tunnel, either in the HV condition ($T_+ = 68.0$, $N = 13$, $P = 0.127$), or in the NS control ($T_+ = 60.0$, $N = 13$, $p = .340$). A comparison of the orangutans' performance in the first and last nine trials revealed that participants spent increasingly less time inspecting the tunnels in the NS control ($T_+ = 80.0$, $N = 13$, $p = .013$), while inspection times did not change in the BO ($T_+ = 50.0$, $N = 13$, $p = .685$) and HV conditions ($T_+ = 50.0$, $N = 13$, $p = .787$).

2.4 Discussion

The first finding is that in the body orientation condition, the orangutans clearly differentiated between the experimenter being oriented towards or away from the tunnels and they preferentially chose the tunnel behind his back (even though they only showed a marginal preference in their initial inspections). Furthermore, they spent more time inspecting the tunnel in front of the experimenter than inspecting the tunnel behind his back. So even when choosing 'wrongly', orangutans were often sensitive to their impending failure. These findings align with previous studies showing that orangutans can clearly differentiate others' attentional states (Kaminski et al., 2004; Liebal, Pika, Call, et al., 2004; Liebal et al., 2006; Poss et al., 2006; Tempelmann et al., 2011). In addition, however, the findings are the first to extend orangutans' ability to determine others' attentional states to a competitive context.

The second finding is that in the critical experimental condition, where the human was facing forwards, the orangutans chose the opaque tunnel marginally more often than the transparent one. Orangutans did not show any preference whatsoever if no competitor was present. This result is very comparable behaviour observed in chimpanzees (Melis et al., 2006). However, contrary to the findings of Melis et al., a direct comparison of the overall performance between conditions revealed no significant differences, indicating that the effect is less clear-cut in orangutans. Furthermore, the orangutans in the current study employed a particular strategy before making their final choice. They frequently inspected the hole before making a choice and sometimes switched sides when they had initially inspected the transparent tunnel (notably, side switches from the opaque to the transparent tunnel were significantly less likely to occur). In addition, they sometimes refrained from opening the transparent tunnel (which was significantly less likely to occur for the opaque tunnel). In their initial inspections the orangutans did not show any preference for either tunnel, and were indifferent in regards to the time they spent inspecting the opaque and the transparent tunnels before making their choice, indicating a lack of sensitivity to whether they made a correct or an incorrect choice in the absence of body orientation cues.

These findings are difficult to reconcile with a full understanding of the human's perspective in the current situation. It could be that orangutans' understanding of a human's perspective is limited and that they need salient cues (e.g., body posture) in order to determine whether or not a human can see them. If the orangutans fully understood which tunnel the human could or could not see, one would expect them to make a choice from their starting point. Instead the orangutans seem to make their choice after arriving at one of the tunnels, and then sometimes decided to switch sides before reaching for the food.

One explanation for this result could be that even though all attempts were made to ensure that participants could not see the human from either tunnel, the orangutans were still able to glimpse the human from the transparent (but not the opaque) tunnel. Therefore, it could be that rather than understanding the human's perspective, the orangutans used an egocentric strategy of inspecting whether the human could be seen from their current side (e.g., the transparent tunnel). If they managed to see the human through the tunnel, they either decided to switch to the other side or refrained from opening the tunnel. I found no increase in performance in any of the behavioural measures in the hidden-visible condition, suggesting that this egocentric rule was not adopted throughout the study (e.g., by associative learning). Also, as the orangutans did not show any preference for the opaque tunnel if no competitor was present, it can be ruled out that their behaviour was driven by a general tendency to retrieve food from visually occluded places (especially as both rewards were actually placed in the open space). Still, the pure presence of the competitor might have been sufficient to trigger this kind of behavioural rule, causing them to follow it without further consideration.

An alternative explanation for the orangutans' differing performance in the body orientation and the hidden-visible condition might be that the body orientation condition was virtually identical to the warm-up trials (except for some added visual barriers). Therefore, the possibility remains that the orangutans simply learned during the warm-up to associate the reward with the experimenter's back as an arbitrary connection and had no understanding of another individual's attention at all. If this were the case, however, it is unlikely, that the participants learned solely during the warm-up phase. As previous studies have demonstrated, apes perform poorly in exploiting arbitrary cues to locate hidden food (e.g., in associating a white coloured bottle with a food reward; see Hanus & Call, 2011). As the number of trials presented during warm-up would have been insufficient to newly acquire a previously arbitrary cue, I rather think that the cue of body orientation was a meaningful stimulus for the orangutans before they participated in the study at hand. Moreover, as all participants were habituated to being fed by their human keepers, they experienced a relatively low level of direct food competition (and if anything were more likely to associate the front of humans with food reward).

In summary the results suggest that orangutans may only have a limited understanding of other's perspectives, relying mainly on salient cues like facial and bodily orientation and body posture. Melis et al. (2006) did not report whether, and how often, their participants switched sides before making a choice and therefore it cannot be completely ruled out that they employed the same strategy as the orangutans. However, in contrast to chimpanzees, for whom a plethora of evidence suggests a sophisticated understanding of others' perspectives, the current results are in line with evidence from other studies that have indicated less distinctive gaze following (Okamoto-Barth et al., 2007) and lower sensitivity to visual attention cues (Liebal, Pika, Call, et al., 2004) in orangutans than in the genus *Pan*. Okamoto-Barth et al. (2007) found orangutans, in contrast to the other great ape species, to be insensitive to whether a barrier was opaque or had a window when tracking the gaze of a human experimenter to a target location. In the study of Liebal, Pika, Call, et al. (2004) orang-utans, requesting food from a human experimenter who had turned around (leaving the food behind her back), also frequently gestured behind the experimenter's back. These, and the current results, seem to be at odds with the findings of Shillito et al. (2005) who reported a single female orangutan to be highly sensitive to the attentional state of a human while directing the human to desirable objects out of the participant's reach. In this task the orangutan had to discriminate between two experimenters, one wearing a bucket over his head, whereas the other had an unimpeded view. Like the orangutans in the hidden-visible condition of the present study, the orangutan could not solve the task by relying on cues from body posture, as the humans were always oriented towards her. However, contrary to the orangutans in my study, she could solve the task egocentrically by basing her judgement on the humans' eyes, which are known to be a very salient cue for attention (reviewed in Emery, 2000). Note, that Kaminski et al. (2004) also found two orangutans that adjusted their food requests according to whether a human had her eyes open or shut. In addition, the orangutan in Shilitio et al.'s study failed to discriminate between opaque and transparent visual barriers, a distinction that my participants essentially needed to make in order to successfully retrieve the food in the hidden-visible condition.

While the sophisticated perspective-taking skills of corvids and chimpanzees presumably represent a case of convergent evolution (Emery & Clayton, 2004), the limited level of perspective-taking in orangutans, as compared to chimpanzees (and humans), suggests that within the great ape clade this capacity may have increased gradually after the human lineage split from our common ancestor. However, it might also be the case that orangutans gradually lost this trait throughout the course of evolution due to their more solitary lifestyle. For instance, ringtailed lemurs, *Lemur catta*, have been found to perform better in gaze following and attention reading tasks than closely related lemur species living in less complex social groups (Sandel et al., 2011). Notably, rhesus macaques, *Macaca mulatta*, competing with a human for food in a series of studies very similar to the present one (Flombaum & Santos, 2005; Santos, Nissen, & Ferrugia, 2006), also took into account what others could see (and hear). However, in a similar way to Shilitio et al.'s study, the macaques might have used the visibility of the human's eyes and gaze direction as discriminative cues to solve the task. Thus, it is possible that the rhesus monkeys were simply avoiding food that had been looked at by a human (see Burkart & Heschl, 2007 for a similar interpretation for marmosets competing against dominant conspecifics for food). Furthermore, there is only little evidence so far that social complexity was a driving factor in the evolution of avian cognition (Emery, 2004; cf. Bond, Kamil, & Balda, 2003, 2007). Another possibility might be that high levels of direct food competition might have driven the development of more sophisticated perspective-taking skills in chimpanzees and corvids, while for a species like orang-utans, with less frequent direct competition for food resources, a limited understanding of others perspectives might be sufficient (note however, that differences to the chimpanzees' peformance in Melis et al. 2006 cannot be explained by motivational reasons, as the orangutans in the present study were nevertheless generally willing and motivated to compete as demonstrated by their performance in the body orientation condition). As yet, the evidence available from different species is too patchy and incomplete to decide on one of these alternative evolutionary trajectories. Future studies, investigating the perspective-taking skills of a wider variety of different species with various experimental paradigms will be required to address this gap. Regarding the great ape clade, studies on gorillas (due to their reduced genetic distance from the *Pan* genera and humans) and Sumatran orangutans, *Pongo abelii*, who have been reported to be more sociable than their Bornean counterparts (Delgado & van Schaik, 2000), might be especially illuminating.

3. Study 2

Infants' and Apes Communication in a Triadic Request Situation

In the present research, I investigated the communicative strategies of 20 month old human infants and great apes when requesting rewards from a human experimenter. Infants and apes both adapted their signals to the attentional state of the experimenter as well as to the location of the reward. Yet, while infants frequently positioned themselves in front of the experimenter and pointed towards a distant reward, apes either remained in the experimenter's line of sight and pointed towards him or moved out-of-sight and pointed towards the reward. Further, when pointing towards a reward that was placed at a distance from the experimenter, only the infants, and not the apes, took the experimenter's attentional state into account. These results demonstrate that prelinguistic human infants and nonhuman apes use different means when guiding others' attention to a location; indicating that differing cognitive mechanisms may underlie their pointing gestures.

3.1 Introduction

While two month old human infants readily engage in dyadic face-to-face interactions, it is not until the age of 9–12 months before they start to communicate about objects and events. This inclusion of external entities into their interactions with others is first achieved through triadic gestures. Triadic gestures are gestures that reference external entities such as objects or events, for instance by showing, offering or pointing (E. Bates, Camaioni, & Volterra, 1975).

E. Bates et al. (1975) classified these early referential gestures as either (proto-) imperative or (proto-)declarative. According to them, infants' imperative gesturing constitutes a kind of social tool use in which others are used as a means to obtain a desired object. Declarative gestures, on the other hand, are used by the gesturing individual to direct the recipient's attention to the referent. This has led some to hypothesize that declarative gestures indicate an understanding of unobservable mental states, whereas employing imperative gestures merely requires an understanding of others as causal agents (e.g., Baron-Cohen, 1989; Mundy, Sigman, Ungerer, & Sherman, 1986; Tomasello & Camaioni, 1997).

Paralleling this distinction between imperative and declarative gestures, there has been a long-running debate whether infant prelinguistic communication is cognitively 'lean' or 'rich' (reviewed in Tomasello, Carpenter, & Liszkowski, 2007). According to a cognitively lean interpretation of infant communication infants initially gesture for selfish reasons and without any deeper understanding of the mental states of others (Barresi & Moore, 1996; D'Entremont & Seamans, 2007). Declarative gesturing and other joint attention behaviours are thought to develop by reinforcement through external rewards such as attaining interesting objects or the adults' attention (Carpendale & Lewis, 2004). Empirical support comes mainly from two lines of evidence. First, imperative pointing seems to emerge before declarative pointing (Camaioni, 1993). Second, infants with autism and infants with Down syndrome, who are known to suffer from socio-cognitive deficits, do not point declaratively but still engage in imperative pointing (Baron-Cohen, 1989; Legerstee & Fisher, 2008).

A rich interpretation of infant communication assumes that from the onset, infants' early gestural communication goes beyond the achievement of material goals and involves an understanding of others as mental agents with their referential intentions aimed at altering and directing the mental states of others (reviewed in Liszkowski, 2011). In this view, the simultaneous appearance of triadic gesturing and other joint attention behaviours indicates a common underlying developmental process—namely the infants' developing understanding of others as mental agents like themselves (Tomasello, 1999). Indeed, when human infants start to point at around 12 months of age, they follow the gaze of others to out-of-sight targets (Deák et al., 2000), around visual barriers (Moll & Tomasello, 2004), check back with the looker if they do not encounter a potential gaze target (Carpenter, Nagell, et al., 1998) and (around 14 months) understand the role of eyes in vision, as well as the occluding properties of blindfolds (Brooks & Meltzoff, 2002).

Overall, these findings suggest that infants at the start of their second year of life understand the gazing of others as 'seeing'. However, much less is known about infants' understanding of others' auditory perception. Moll, Carpenter, and Tomasello (2014) found that 2-year-olds know what others have heard in the immediate past based on previous episodes of joint auditory attention. Two-year-olds in a study of Williamson, Brooks, and Meltzoff (2015) produced higher intensity sounds when prompted to wake a doll whereas they produced lower intensity sounds after being told not to wake the doll. In a study of Melis, Call, and Tomasello (2010), 3-year-olds, in the presence of an adult, preferentially retrieved a prohibited toy through a silent door instead of a noisy door (which had a bell attached to it). However, to my knowledge, no study so far directly investigated whether infants employ auditory gestures or vocalizations to attract attention in a communicative context.

For nonhuman great apes (henceforth apes), it has also been debated whether they gesture to influence others' mental states, or alternatively, to simply influence others' behaviour. Apes flexibly use a particular gesture across different functional contexts and a variety of gestures to achieve the same end in a specific context (Plooij, 1978). When pursuing a communicative goal, they show persistence as well as elaboration of their gestures (Leavens, Russell, & Hopkins, 2005). Further, apes understand that recipients have to be perceptually attentive for a signal to be effective and adapt their visual signals accordingly (Hostetter et al., 2001; Povinelli & Eddy, 1996b; Tempelmann et al., 2011). The evidence that apes use auditory signals as attention getters is mixed, although Melis et al. (2006) found that chimpanzees preferentially retrieved a contested piece of food through a silent door instead of a noisy one if a human competitor was present, suggesting that they might be aware of others' auditory perception capacities (cf. Bräuer, Call, & Tomasello, 2008). Similarly, apes have been evidenced to respond to an inattentive recipient with an increase in auditory response measures (Hostetter et al., 2001; Hostetter et al., 2007; Leavens, Hostetter, Wesley, & Hopkins, 2004; Leavens et al., 2010). However, other studies found no effects of the recipient's orientation on auditory signaling (Liebal, Pika, Call, et al., 2004; Tempelmann et al., 2011) or a decrease of auditory signals in response to an inattentive recipient (J. L. Russell et al., 2005; Tomasello, Call, Nagell, Olguin, & Carpenter, 1994). While apes demonstrate a generally high degree of flexibility in their gestural communication, their gesturing appears to mostly serve imperative purposes. This also includes ape manual pointing (henceforth 'pointing').

Whereas pointing is only rarely observed in the wild (cf. Douglas & Moscovice, 2015), captive apes sometimes spontaneously acquire the pointing gesture (i.e., without any explicit training). However, most apes exclusively point for human caregivers, but only rarely for other conspecifics (reviewed in Hobaiter, Leavens, & Byrne, 2014). Further, ape pointing usually occurs either as a direct imperative request for food or as indirect imperative request for tools that are instrumental in retrieving food (Bullinger, Zimmermann, Kaminski, & Tomasello, 2011; Zimmermann et al., 2009), with the exception of home reared and language-trained apes who have also been reported to engage in declarative pointing (reviewed in Leavens & Bard, 2011); albeit that imperative requests apparently constitute the major part of their communication (Rivas, 2005). Moreover, standard-reared captive apes' failure to comprehend pointing cues in the object-choice task, in which a human experimenter points to the one container out of several possible that is holding hidden food, casts doubt on a cognitive rich interpretation of ape pointing (see Lyn, Russell, & Hopkins, 2010 also for contradictory results with language-trained apes). Nevertheless, the high level of sophistication that apes show in their gestural communication has led some researchers to claim that "pointing, per se, does not require cognitive adaptations that are unique to humans" (Hobaiter et al., 2014, p. 86); that apes gesture referentially, and that these gestures can be considered triadic (e.g., indicated by gesturing for the most desirable food; Leavens, Hopkins, & Thomas, 2004).

Although developmental and comparative psychologists tend to classify pointing and other gestures as either imperative or declarative, some studies indicate that this distinction might be artificial and that infants' imperative requests sometimes include an attempt to influence others' mental states (Grosse, Behne, Carpenter, & Tomasello, 2010; Shwe & Markman, 1997). Therefore, as indicated by Halina (2016), from a cognitive perspective it might be more fruitful to characterize pointing (and other gestures) according to whether or not it constitutes a deliberate attempt to direct the gaze of others (to an external entity). However, if the external entity is constantly in the attentional focus of the recipient, as is the case in most studies on pointing production with apes where the location of the food and the recipient is identical, there is no need to direct attention via gestures. Thus, in such a triadic request situation it remains ambiguous whether the apes only point to receive the food or (also) to direct the recipient's attention.

One notable exception where the recipient was at a separate location than the referent is the study of Roberts, Vick, Roberts, and Menzel (2014) in which two language-trained chimpanzees used their gestures to guide a human helper to distant hidden food. Whereas both chimpanzees increased the frequency of their gesturing when the human approached the food, only one of the two actually pointed in the direction of the food. Yet, due to the repeated turn-taking and communicative interactions with the human, it remains unclear whether the apes were attempting to direct the human's attention towards the food (or were just responding to behavioural and positional cues to maneuver the human to the reward location). Furthermore, the results of the only other study investigating apes' communication in a situation in which food and experimenter were at separate locations (Leavens et al., 2015) are difficult to compare to other studies (e.g., van der Goot, Tomasello, & Liszkowski, 2014). This is due to the lack of control conditions examining apes' performance (1) in a situation in which the experimenter and the food were at the same location or (2) in a situation in which the experimenter was inattentive. Further, whereas plenty of studies have established that infants point to direct (and share) attention, only a minority has investigated whether this also holds true for infants gestural requests (cf. Grosse et al., 2010; Shwe & Markman, 1997).

Thus, to explore the communicative strategies of prelinguistic human infants and great apes in a comparable triadic request situation, I conducted a study in which I systematically varied the location of the referent (i.e., the reward) relative to the experimenter (the reward and experimenter either being separated by an opaque barrier or not), as well as the experimenter's visual attention (the experimenter either facing towards the participant or not) in a two by two factorial design. I expected participants to adapt their signals to the attentional state of the experimenter (e.g., by producing less visual gestures and more auditory signals when the experimenter was facing away). If some of the participants' requests constituted a deliberate attempt to direct the experimenter's attention to the reward, I was expecting participants to employ these communicative signals in such ways that they were not only visible to the experimenter, but that they were also specifically targeted towards the reward. Thus, when the experimenter was separated from the reward, to qualify as triadic the respective signal should be (1) directed at the experimenter, but also (2) targeted towards the reward (instead of towards the experimenter). Participants' performance in the conditions in which experimenter and the reward were located on the same side will help to contrast the results with unambiguously triadic conditions (i.e., when the reward was placed separately from the experimenter) to the results of other studies. As Menzel (49) suggested inconspicuous body pointing to be a possible mechanism for referential communication in chimpanzees, we analysed participants' movement between sides ('switches') in addition to their gestural and auditory signaling.

3.2 Methods

Participants. Forty-one human infants were recruited through the child laboratory of the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany. Seventeen infants had to be excluded: 14 of them lost interest in the toy apparatus that served as motivational incentive for requesting reward before completing one session of all four experimental conditions, and three due to experimenter error. The final dataset consisted of a total of 12 boys and 12 girls with a mean age of 19.94 months (*SD* = 0.30 months; range: 19.48–20.47 months). The infants were tested individually in the presence of a parent in a silent room at the institute, in which they were allowed to move freely (i.e., infants were not restrained by being seated on the parent's lap or on a chair). Parents were instructed to refrain from any verbal or non-verbal cuing. Informed written consent was obtained from all the parents of the infants who participated in this study. The study was non-invasive and adhered to all appropriate German ethical and legal protocols. Furthermore, the study procedure was approved by the Ethics Committee of the Max Planck Institute for Evolutionary Anthropology Ethics Committee.

Thirty-two apes, housed at the Wolfgang Köhler Primate Research Centre in Leipzig, Germany, participated in the study. Participants were five bonobos, *Pan paniscus*, (two females, three males), 18 chimpanzees, *Pan troglodytes* (13 females, five males), three gorillas, *Gorilla gorilla* (three females), and six orangutans, *Pongo pygmaeus* (five females, one male). Participants' mean age was 17.8 years (*SD* = 9.7 years; range: 4.4–34.9 years). Groups of apes were housed in semi-natural indoor and outdoor enclosures with regular feedings, daily enrichment and water was available ad libitum. Participants voluntarily participated in the study and were tested individually (or with their dependent offspring) in familiar sleeping or observation rooms. Research at the WKPRC was performed in accordance with the recommendations of the Weatherall report 'The use of nonhuman primates in research' (Weatherall, Bell, Blakemore, Ludlow, & Walport, 2006) and strictly adhered to the legal requirements of Germany. No medical, toxicological or neurobiological research of any kind is conducted at the WKPRC. The full procedure of the study was approved by the Max Planck Institute for Evolutionary Anthropology Ethics Committee. Animal husbandry and research comply with the 'EAZA Minimum Standards for the Accommodation and Care of Animals in Zoos and Aquaria', the 'WAZA Ethical Guidelines for the Conduct of Research on Animals by Zoos and Aquariums' and the 'Guidelines for the Treatment of Animals in Behavioural Research and Teaching' of the Association for the Study of Animal Behaviour (ASAB). IRB approval was not necessary because no special permission for the use of animals in purely behavioural or observational studies is required in Germany. Further information on this legislature can be found in paragraphs 7.1, 7.2 and 8.1 of the German Protection of Animals Act ('Tierschutzgesetz').

Experimental set-up. Two containers were used (approximately 1.5 m apart), one of them holding a reward and the other one remaining empty (see Fig. 5). Participant and experimenter (E_1) were separated by a transparent barrier allowing participants to see both containers but not to reach them. The experimenter's area was split in half by another, visually opaque, barrier, blocking the line of sight between the experimenter's side and the other side.

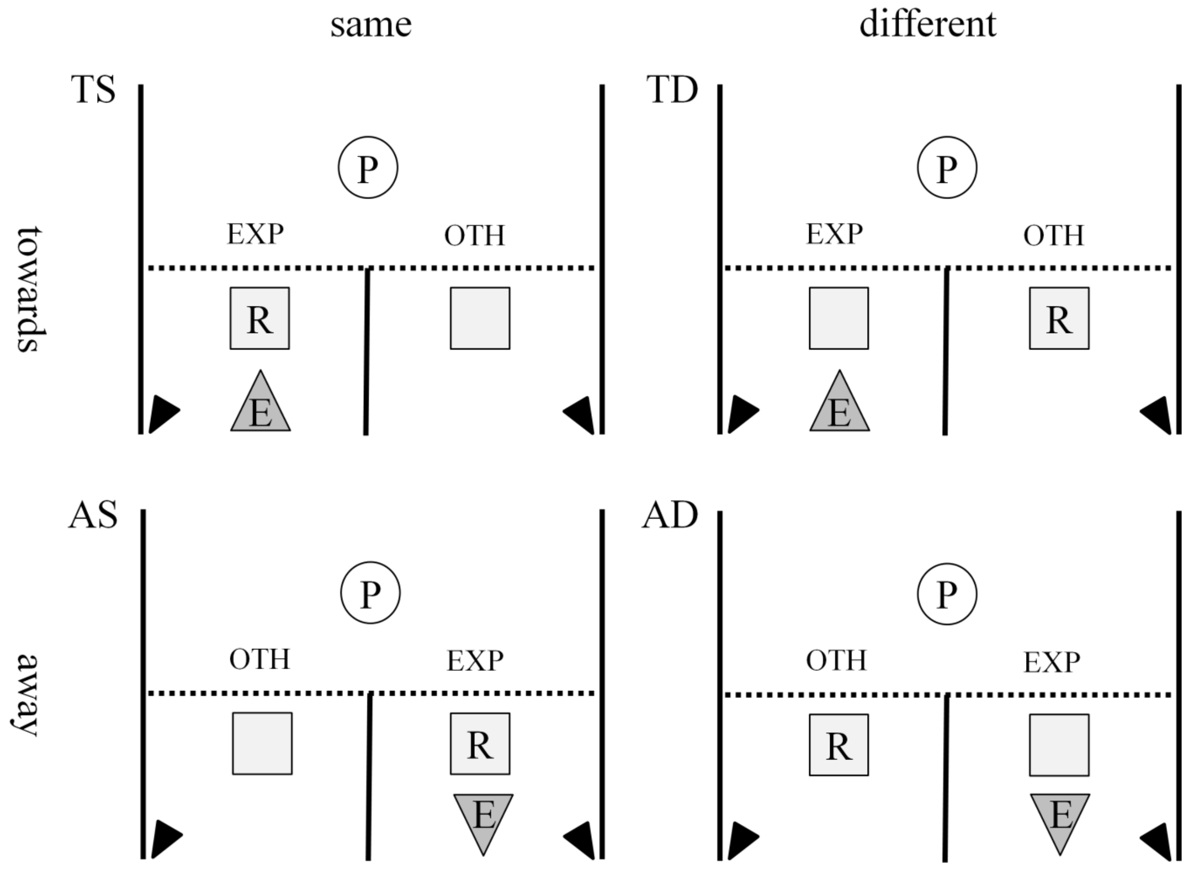

Figure 5. Experimental set-up in all conditions (R: reward; E: experimenter; P: participant; dotted line: transparent barrier; central solid line: opaque visual barrier; squares: containers; black triangles at the bottom left and right corners: cameras). In a two by two study design I varied whether the experimenter was oriented towards the participant (upper row; indicated by a triangle facing upwards) or away from the participant (lower row; indicated by a triangle facing downwards) and whether the experimenter and the reward were located on the same side (left column) or on different sides (right column) resulting in the four experimental conditions towards-same (TS), towards-different (TD), away-same (AS) and away-different (AD); EXP: experimenter side, OTH: other side

Infants were rewarded with coloured wooden blocks that they could put down a chute to elicit sounds from a toy apparatus held by a second experimenter (E_2) at the far end of the room. Both E_1 and E_2 were unfamiliar to all infants. Two cardboard boxes were used as containers to stash the blocks. As pilot testing revealed that infants had difficulties to remember where the reward was hidden, the boxes were left open and placed with the top opening facing the participant. Thus, the infant (but not E_1) was able to see the blocks in warm-up as well as experimental trials. The transparent plexiglass barrier was 80 cm high with a narrow gap in the midst of each side to facilitate the transfer of blocks between experimenter and infant. Before entering the testing room the infants became acquainted with both experimenters in a short warm-up play (of about 10 min duration) with various toys unrelated to the study.

Apes received food as reward. Opaque plastic cups were used as containers to hide food pieces. The transparent plexiglass barrier had two small holes on each side allowing the apes to indicate their choice of cups. E_1 and E_2 were familiar to all apes because of previous studies.

Warm-up trials. Prior to testing, all participants received a series of warm-up trials to accustom themselves to the general setup and procedure of the task. Participants were familiarized with requesting a reward from the experimenter as well as the fact that rewards could be obtained on both sides of the barrier.

The infants' warm-up started with E_1, E_2, and the infant conjointly exploring the toy apparatus. After a brief introduction into its functionality, E_1 entered the experimenter's area and sat down on the right side of the opaque barrier (from E_1's perspective) oriented towards the infant. E_1 responded to the infant's gestural requests by handing over blocks (one at a time) until the container was empty. The same procedure was repeated on the left side of the opaque barrier. In total, infants received six blocks from E_1 (three on each side). If infants did not spontaneously request blocks, E_2 verbally encouraged them to do so, occasionally also guiding them to E_1 and the container.

Ape warm-up trials started with E_2 placing a piece of food under one of two cups (both positioned either on the right side or the left side of the opaque barrier) in full sight of the participant. After E_2 had left the room, E_1 entered and sat down in front of the cups, with his face and body turned towards the participant. Participants had only one chance to indicate their choice of cups. They only received the food reward if they chose the baited cup. Subsequently, E_1 left and E_2 re-entered to set up the next trial. Participants received a total of six warm-up trials (three on the left side and three on the right side of the opaque barrier). In half of the trials the reward was placed under the right cup, in half of the trials it was placed under the left cup. Warm-up trials were semi-randomized such that no more than two consecutive trials were conducted on the same side. Likewise, neither could the reward be retrieved from the same cup in more than two consecutive trials.

Experimental trials. In the experimental trials I systematically varied the two factors of (whole body) orientation and location (in regards to the reward) in a two by two study design. E_1 could be oriented either *towards* the participant or *away* from the participant and E_1 and the reward could be either located on the *same* side or on *different* sides of the visual barrier (see Fig. 5). This resulted in the following four experimental conditions.

(1) ***towards-same (TS).*** E_1 was facing the participant and E_1 and the reward were both located on the experimenter's side.

(2) ***towards-different (TD).*** E_1 was facing the participant and located on the experimenter's side whereas the reward was located on the other side.

(3) ***away-same (AS).*** E_1 was oriented 180 degrees away from the participant and E_1 and the reward were both located on the experimenter's side.

(4) ***away-different (AD).*** E_1 was oriented 180 degrees away from the participant and located on the experimenter's side whereas the reward was located on the other side.

During trials, E_1 maintained the initially assumed posture and position, acted neutrally (i.e., by performing slight movements or producing humming sounds to make the situation more natural) and never responded to any of the participant's behaviour. Furthermore, E_1 avoided direct eye contact with the participant during testing, as eye contact itself is known to be a strong communicative cue (Emery, 2000). After the trial duration had elapsed, E_1 revealed the content of the container that the participants showed the strongest interest in (indicated by their position and communicative behaviour). Participants received non-differential reinforcement, that is, E_1 always retrieved and transferred the reward from the baited container, either directly (when participants chose correctly) or after first revealing the empty container (when participants chose incorrectly). E_1 then left the scenery while E_2 set up the next trial. All participants completed at least one session, each consisting of four trials (one per condition). The order of conditions within a session was counterbalanced across participants.

For infants eight trials were administered, split up in two consecutive sessions on the same day. Trial duration was 20 s. While 12 out of 24 infants completed both sessions, the others completed only the first session fully and the second session partially (average number of trials completed = 6.8; *SD* = 1.4).

For apes, 16 trials were administered, each lasting 30 s, on two separate days with two consecutive sessions on each day. On both days, apes received a warm-up prior to testing and two additional motivational trials in-between the two sessions. Motivational trials were identical to warm-up trials, with one of them being administered at each side.

Coding. All trials were recorded by digital camcorders from different angles (one camera recording on each side for infants, two per side for apes: one recording at the ground level, one recording at the upper ceiling level of the testing area) and subsequently scored from the video files. I coded a total of 15 different communicative behaviours (see Appendix B.1), the side where participants were located at when producing the behaviour (‘side of production’), and towards which ‘target side’ it was directed. The three possible values for ‘Side’ were ‘experimenter’s side’ (i.e., the side where E_1 was located), ‘other side’ (i.e., the side that E_1 could not see), and ‘middle’ (i.e., the area in-between sides; a participant was scored as being in the middle position when its body parts were spanning the experimenter’s side as well as the other side). To exclude interactions with other communicative partners than the experimenter (e.g., with a parent or E_2), a behaviour was only scored if the participant was oriented towards the experimenter’s area (i.e., experimenter’s side, other side, or the middle). For analysis, I categorized the 15 different behaviours according to their main mode of perception: auditory signals and visual gestures. As Menzel (1973) suggested inconspicuous body pointing to be a possible form of referential communication in chimpanzees, I also scored two positional measurements. These were movements from one side to the other (‘switches’), and the time each participant spent on either side (‘duration of stay’). A second coder, blind to the experimental condition, coded the participants’ behaviour in 18% of all conducted trials. Agreement between coders was 85% for behaviour types (Cohen’s $\kappa = .77$), 96% for sides of production ($\kappa = .92$), and 98% for target sides towards that apes directed their gestures ($\kappa = .97$). Intraclass correlation for the duration of stay was ICC(1,1) = .92.

Analysis. One of the goals of the study was to investigate whether apes and infants exhibit a preference to signal in close proximity to the reward (van der Goot et al., 2014), or whether they show no such preference (Leavens et al., 2015). Therefore, I explored for each condition whether participants spent more time, or produced more auditory and visual gestures on the experimenter's side or on the other side. Wilcoxon signed-rank tests were employed to conduct within condition across side comparisons for each of the three aforementioned behavioural measurements.

Further, the variation of the number of side switches as well as auditory and visual signals and pointing gestures was analysed separately for each side. For auditory signals and visual gestures, I analysed the *side of production* (i.e., where participants were located during their request); for side switches and pointing, I analysed *target sides* (i.e., towards which sides participants directed these behaviours). If possible, I assessed the overall and main effects of the three predictor variables species (human vs. ape), orientation (towards vs. away), and location (experimenter's side vs. other side) as well as their interaction via a Generalized Linear Mixed Model (GLMM). If a GLMM indicated a significant interaction between the test factors orientation and location, follow-up pairwise comparisons via Wilcoxon signed-ranks tests were conducted across each one of the factors while the other was held constant. As I was primarily interested in whether the test factors orientation and location differentially affected infants' and apes' behaviours and less interested in absolute differences between species (which also might have been due to differences in the experimental procedures), post hoc analyses for interactions involving the factor species were only conducted within and not across species. As the data for the number of pointing gestures directed towards the other side was too sparse to run a GLMM analysis (leading to a convergence failure within 100,000 iterations), I used Wilcoxon signed-ranks tests to compare the factors orientation and location separately for each species.

GLMM full models included the three main factors species, orientation and location, their interaction, the fixed control variables sex and (z-transformed) trial order and, to control for random by-participant variation, the random effect as well as the random slopes of participants. All analyses were conducted using the statistic software R (R Core Team, 2014). The count data was modeled with a Poisson distribution via the lme4-package (D. Bates, Maechler, Bolker, & Walker, 2015).

To test the overall significance of the two test factors, likelihood ratio tests (based on the -2LL values of the respective models) were used to compare the full model to a null model containing only the control variables and random slopes (Forstmeier & Schielzeth, 2011). All full models that differed significantly from their respective null models were compared to a reduced model that did not include the three-way interaction of the test factors but was otherwise identical to the corresponding full model. Subsequently, the reduced model containing all two-way interactions was compared to reduced models that lacked one of the three two-way interactions (but were otherwise identical). Non-significant interactions were removed from the model to interpret lower-order effects. Throughout the results section by referring to 'participants' we denote the combined datasets of apes and infants.

The ape sample sizes (with all species except for chimpanzees being composed by as few as six or less individuals) prevented me from including species as a five level categorical factor in the GLMMs and conducting (meaningful) post hoc comparisons separately for each ape species. However, I additionally ran all analyses with a reduced ape sample restricted to the two *Pan* species (see Appendix B.2–B.8). If not stated otherwise these analyses did not yield differing results from the analyses combining all nonhuman genera as 'apes'.

3.3 Results

First, I will present the analysis of the two positional measurements 'duration of stay' and 'side switches'. I will then focus on the production of auditory and visual signals, and conclude the results section by analyzing to which target sides participants directed their pointing gestures.

Duration of stay. For infants, across side comparisons revealed that they stayed significantly longer on the experimenter's side if the reward was located on the same side (Wilcoxon signed-ranks test; TS: $T_+ = 254.0$, $N = 23$, $p < .001$; AS: $T_+ = 214.0$, $N = 22$, $p = .003$). When the experimenter and the reward were located on different sides, infants showed no preference for either side (TD: $T_+ = 145.0$, $N = 21$, $p = .320$; AD: $T_+ = 119.5$, $N = 20$, $p = .601$). Apes stayed significantly longer on the experimenter's side if the reward was located on the same side (TS and AS: $T_+ = 528.0$, $N = 32$, $p < .001$). If reward and experimenter were located on different sides, apes preferred to stay on the other side, that is, with the reward (TD: $T_+ = 413.0$, $N = 32$, $p = .004$; AD: $T_+ = 450.0$, $N = 31$, $p < .001$).

Switches. A Poisson GLMM indicated a significant overall effect of the three test factors on the number of switches to the experimenter's side (likelihood ratio test: $\chi^2 = 48.16$, $df = 7$, $p < .001$; see Fig. 6). This was due to a significant interaction of orientation and location ($\chi^2 = 5.43$, $df = 1$, $p = .020$; see Appendix B.2) and apes switching to the experimenter's side more often than infants (main effect of species: 0.53 ± 0.26, $p = .038$). Post hoc pairwise comparisons within orientation revealed that participants switched more often to the experimenter's side when the experimenter and the reward were located on different sides (Wilcoxon signed-ranks test; TS–TD: $T_+ = 755.0$, $N = 43$, $p < .001$; AS–AD: $T_+ = 414.0$, $N = 32$, $p = .003$). Comparisons within location indicated no significant differences across orientation (TS–AS: T_+ = 172.5, N = 24, p = .526; TD–AD: T_+ = 456.0, N = 37, p = .114).

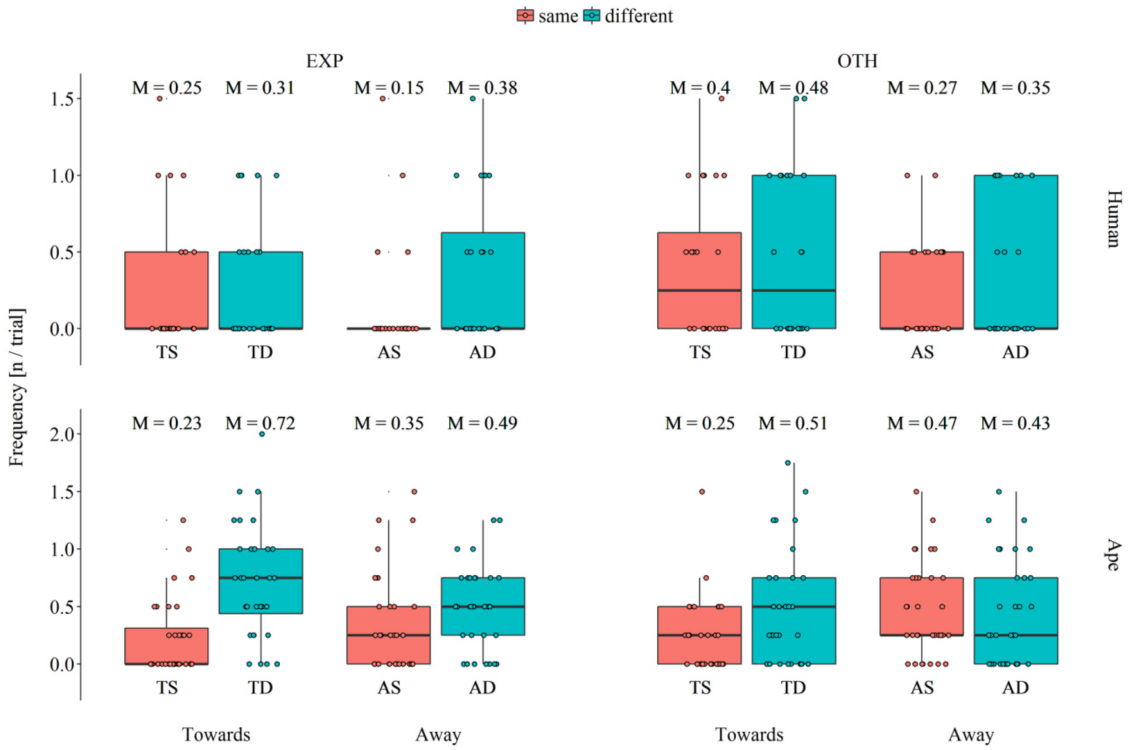

Figure 6. Box plot of the average number of times per trial that human infants (upper row) and apes (lower row) switched to the experimenter's (EXP: left column) and the other side (OTH: right column) across the factors orientation (Towards: two leftmost boxes in each plot, Away: two rightmost boxes in each plot) and location (red: experimenter and reward are on the same side, blue: experimenter and reward are on different sides) resulting in the four experimental conditions towards-same (TS), towards-different (TD), away-same (AS) and away-different (AD); M: condition mean value, the middle line of each box represent population median values (different from the M above each box); lower and upper hinges display first and third quartiles, respectively; whiskers extend up to 1.5 x interquartile range, small circles represent individual data points.

A second Poisson GLMM also indicated a significant overall effect of the three test factors on the number of switches to the other side (likelihood ratio test: χ^2 = 15.93, df = 7, p = .026), due to a significant interaction of orientation and location (χ^2 = 6.19, df = 1, p = .013; see Appendix B.3). Post hoc pairwise comparisons across location revealed that within the two *towards* conditions, participants switched more often to the other side when the experimenter and the reward were located on different sides (Wilcoxon signed-ranks test; TS–TD: $T_+ = 535.0$, $N = 38$, $p = .015$), whereas there was no such difference when the experimenter was inattentive (AS–AD: $T_+ = 238.5$, $N = 30$, $p = .896$). Comparisons within location indicated no significant differences across orientation (TS–AS: $T_+ = 320.0$, $N = 31$, $p = .178$; TD–AD: $T_+ = 317.0$, $N = 31$, $p = .178$).

Auditory signals. Across sides, infants produced significantly more auditory signals on the experimenter's side in three out of four conditions (TS: $T_+ = 91.0$, $N = 13$, $p < .001$; TD: $T_+ = 129.5$, $N = 17$, $p = .010$; AS: $T_+ = 93.0$, $N = 14$, $p = .008$). In the AD condition, infants showed no preference for either side ($T_+ = 78.5$, $N = 15$, $p = .307$). Apes produced more auditory signals at the experimenter's side when the reward was on the same side (TS: $T_+ = 231.0$, $N =21$, $p < .001$; AS: $T_+ = 160.0$, $N = 18$, $p < .001$), whereas they showed no preference for either side in the TD condition ($T_+ = 20.5$, $N = 8$, $p = .805$) and produced more auditory signals on the other side in the AD condition ($T_+ = 58.5$, $N = 11$, $p = .020$). The latter difference only resulted in a trend when just the two *Pan* species were considered ($T_+ = 31.0$, $N = 8$, $p = .078$).

A Poisson GLMM analysis indicated a significant overall effect of the test factors on the number of auditory signals that participants produced on the experimenter's side (likelihood ratio test; $\chi^2 = 53.45$, $df = 7$, $p < .001$). This was due to a significant interaction of species and location ($\chi^2 = 13.84$, $df = 1$, $p < .001$; see Appendix B.4) and a trend to produce more auditory signals when the experimenter was oriented towards the participants (main effect of orientation: 0.34 ± 0.20, $p = .098$). When only the two *Pan* species were included, the latter difference resulted in a significant effect (main effect of orientation: 0.45 ± 0.20, $p = .029$). Post hoc pairwise comparisons across location revealed that apes produced more auditory signals on the experimenter's side when the reward was located on the same side

(Wilcoxon signed-ranks test; $T_+ = 253.0$, $N = 22$, $p < .001$), whereas no such difference was found for infants ($T_+ = 132.0$, $N = 21$, $p = .579$).

A second Poisson GLMM analysis also indicated a significant overall effect of the test factors on the number of auditory signals that participants produced on the other side (likelihood ratio test; $\chi^2 = 64.68$, $df = 7$, $p < .001$). This was due to a interaction of species and orientation ($\chi^2 = 3.89$, $df = 1$, $p = .048$; see Appendix B.5) that turned to a trend when the ape sample was restricted to include only the two *Pan* species ($\chi^2 = 2.51$, $df = 1$, $p = .078$), and participants producing more auditory signals on the other side when the experimenter and the reward were located on different sides (main effect of location: -4.09 ± 1.95, $p = .036$). Post hoc pairwise comparisons indicated that neither infants nor apes differed in the number of auditory signals produced on the other side across orientation (Wilcoxon signed-ranks test; infants: $T_+ = 40.0$, $N = 10$, $p = .229$; apes: $T_+ = 75.5$, $N = 14$, $p = .169$).

Visual gestures. Across sides, infants produced a higher number of visual gestures on the experimenter's side in three out of four conditions (TS: $T_+ = 105.0$, $N = 14$, $p < .001$; TD: $T_+ = 53.0$, $N = 10$, $p = .008$; AS: $T_+ = 41.0$, $N = 9$, $p = .027$; see Fig. 7). In the AD condition they showed no preference for either side ($T_+ = 35.0$, $N = 11$, $p > .922$). Apes exhibited a preference to produce visual gestures in proximity to the reward, that is, they visually gestured more frequently on the experimenter's side when the reward was located on the same side (TS: $T_+ = 528.0$, $N = 32$, $p < .001$; AS: $T_+ = 458.0$, $N = 30$, $p < .001$), whereas they produced more visual gestures on the other side when the experimenter and the reward were located on different sides (TD: $T_+ = 363.0$, $N = 31$, $p = .023$; AD: $T_+ = 383.0$, $N = 28$, $p < .001$). If the analyses were restricted to the two *Pan* species, the difference across sides in the TD condition turned into a trend (TD: $T_+ = 193.5$, $N = 23$, $p = .093$).

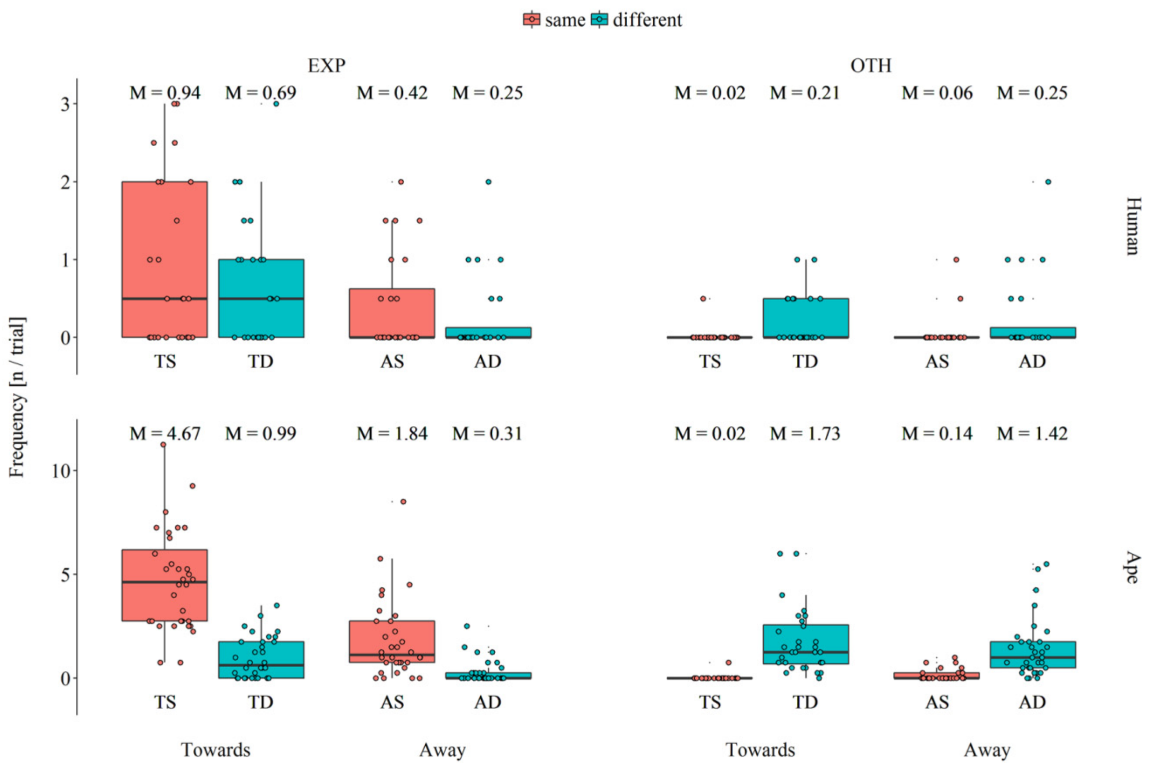

Figure 7. Box plot of the average number of visual gestures per trial that human infants (upper row) and apes (lower row) produced on the experimenter's side (EXP: left column) and the other side (OTH: right column) across the factors orientation (Towards: two leftmost boxes in each plot, Away: two rightmost boxes in each plot) and location (red: experimenter and reward are on the same side, blue: experimenter and reward are on different sides) resulting in the four experimental conditions towards-same (TS), towards-different (TD), away-same (AS) and away-different (AD); M: condition mean value, the middle line of each box represent population median values (different from the M above each box); lower and upper hinges display first and third quartiles, respectively; whiskers extend up to 1.5 x interquartile range, small circles represent individual data points.

A Poisson GLMM indicated a significant overall effect of the test factors on the number of visual gestures that participants produced on the experimenter's side (likelihood ratio test; $\chi^2 = 103.85$, $df = 7$, $p < .001$). This was due to a significant interaction of species and location ($\chi^2 = 20.39$, $df = 1$, $p < .001$; see Appendix B.6) and participants visually gesturing more frequently when the experimenter was oriented towards them (main effect of orientation: 1.07 ± 0.13, $p < .001$). Post hoc pairwise comparisons indicated that apes produced more visual gestures on the experimenter's side when the reward was located on the same side (Wilcoxon signed-ranks test; $T_+ = 496.0$, $N = 31$, $p < .001$), whereas no such difference was found for infants ($T_+ = 114.0$, $N = 18$, $p = .223$).

A second Poisson GLMM revealed that the test factors also had a significant overall effect on the number of visual gestures that participants produced on the other side (likelihood ratio test; $\chi^2 = 124.97$, $df = 7$, $p < .001$), due to a significant interaction of orientation and location ($\chi^2 = 14.41$, $df = 1$, $p < .001$; see Appendix B.7) and apes producing more visual gestures than infants (main effect of species: 1.83 ± 0.35, $p < .001$). Post hoc pairwise comparisons within orientation revealed that participants produced more visual gestures on the other side when the experimenter and the reward were located on different sides (TS–TD: $T_+ = 741.0$, $N = 38$, $p < .001$; AS–AD: $T_+ = 603.5$, $N = 35$, $p < .001$). Comparisons across orientation indicated that participants within the two same conditions produced more visual gestures on the other side when the experimenter was oriented away (Wilcoxon signed-ranks test; TS–AS: $T_+ = 66.0$, $N = 12$, $p = .033$). Pairwise comparisons within the two different conditions indicated no significant differences across orientation (TD–AD: $T_+ = 370.0$, $N = 34$, $p = .218$).

Pointing. As the goal of the present study was to investigate triadic communication, I ran additional analyses on the number of pointing gestures that participants produced in the experimenter's line of sight (i.e., on the experimenter's side or in the middle in-between sides). Contrary to the previous analyses, the following analyses focus on the target sides to which participants pointed instead of the sides where they produced the pointing gestures.

A Poisson GLMM indicated a significant overall effect of the test factors on the number of pointing gestures that participants directed towards the experimenter's side ($\chi2 = 122.17$, $df = 7$, $p < .001$; see Fig. 8). This was due to all participants pointing more frequently towards the experimenter's side when the experimenter was oriented towards them (main effect of orientation: 1.04 ± 0.12, $p < .001$; see Appendix B.8) and when the reward was located on the same side (main effect of location: 1.40 ± 0.12, $p < .001$). Furthermore, apes pointed more frequently to the experimenter's side than infants (main effect of species: 1.99 ± 0.28, $p < .001$).

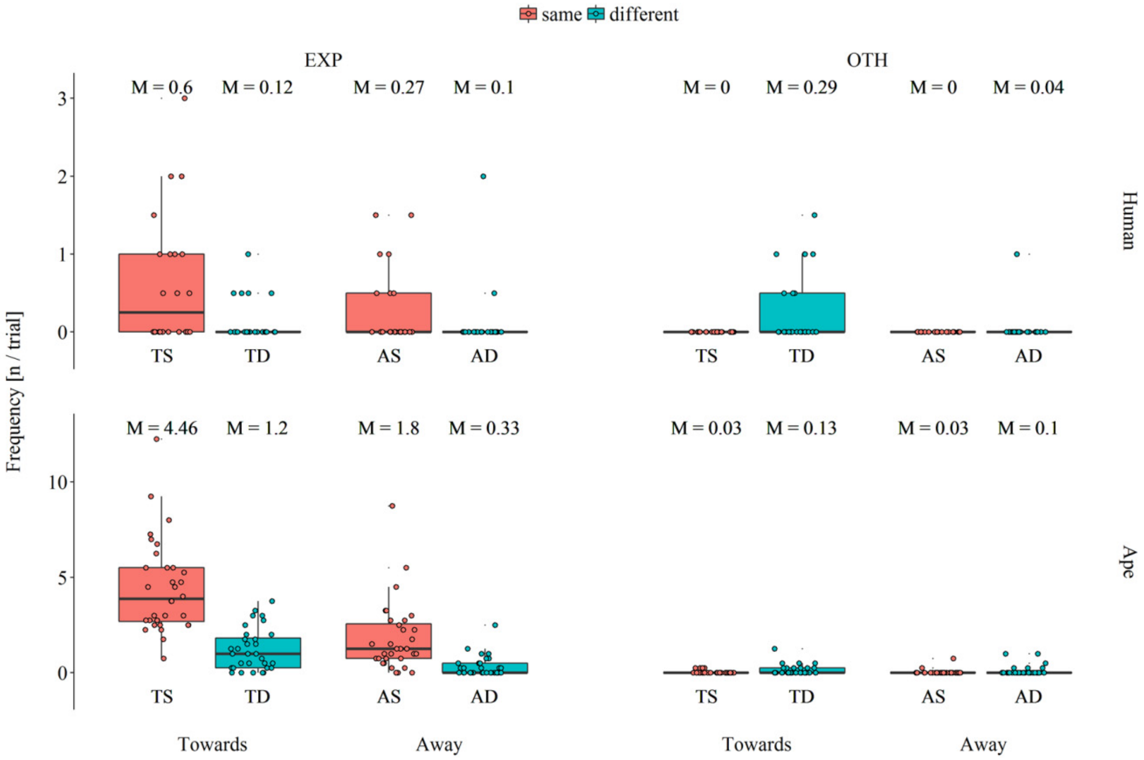

Figure 8. Box plot of the average number of pointing gestures per trial that human infants (upper row) and apes (lower row) directed towards the experimenter's side (EXP: left column) and the other side (OTH: right column) across the factors orientation (Towards: two leftmost boxes in each plot, Away: two rightmost boxes in each plot) and location (red: experimenter and reward are on the same side, blue: experimenter and reward are on different sides) resulting in the four experimental conditions towards-same (TS), towards-different (TD), away-same (AS) and away-different (AD); M: condition mean value, the middle line of each box represent population median values (different from the M above each box); lower and upper hinges display first and third quartiles, respectively; whiskers extend up to 1.5 x interquartile range, small circles represent individual data points.

As the GLMM for the number of pointing gestures that participants directed towards the other side failed to converge, I instead conducted within species pairwise comparisons across each of the two factors location and orientation. Whereas infants and apes both pointed more frequently towards the other side when the reward was located there (Wilcoxon signed-ranks test; infants: $T_+ = 45.0$, $N = 9$, $p = .004$; apes: $T_+ = 59.5$, $N = 11$, $p = .018$), only infants exhibited a marginal trend to direct more pointing gestures towards the other side when the experimenter was attentive (Wilcoxon signed-ranks test; infants: $T_+ = 39.0$, $N = 9$, $p = .051$; apes: $T_+ = 40.0$, $N = 11$, $p = .544$).

3.4 Discussion

Infants’ positioning as well as their production of auditory signals and visual gestures on the other side (which was out-of-sight for the experimenter in all conditions) was foremost driven by the reward location. Nevertheless, they generally exhibited a strong preference to request the reward at the experimenter’s side. Infants did not increase the frequency of their auditory signals to attract the attention of the experimenter when he was oriented away. They did, however, exhibit a marginal trend to increase the frequency of their auditory signals when the experimenter was inattentive. A likely explanation for this finding might be that vocalizations, which constituted a major part of all auditory signals produced by infants (256 of 288), occurred frequently in conjunction with pointing and other visual gestures. Thus, instead of employing them as attention getters, infants seemed to use their vocalizations (that often were single word utterances as “hier” [here] and “da” [there]; 104 occurrences produced by 12 different infants) as a means to highlight and clarify the referent of their gesturing. Nevertheless, the effect of the experimenter’s attention on infants’ auditory signals was less pronounced than for their visual gestures, which is in accordance with expectation.

While infants adapted their production of visual gestures on the experimenter’s side to the attentional state of the experimenter, their visual gesturing remained unaffected by the location of the reward. This was due to infants also pointing in the experimenter’s line of sight when the reward was located on the other side. In contrast, apes preferentially approached the reward before pointing. Furthermore, infants adapted the direction of their pointing towards the experimenter's and the other side in accordance with the location of the reward as well as the experimenter's attentional state. Therefore, one can rule out the possible explanation that this behaviour arose merely from the experimenter and the reward being in separate locations. One could argue that the infants were trying to command the experimenter to the reward location. However, this is not reflected by the single word utterances that frequently accompanied their pointing and that were never verbs or commands (like "gib" [give] or "geh" [go]), but only indicatives (e.g., "hier" [here], "da" [there]). This indicates that the infants' pointing was triadic and constituted a communicative effort to inform the experimenter about the whereabouts of the reward.

This result is in line with a cognitive rich interpretation of infant pointing. Recent studies have not only found various prosocial motives for infant pointing such as providing helpful information (Liszkowski, Carpenter, Striano, & Tomasello, 2006), warning others (Knudsen & Liszkowski, 2012c), and sharing interest in objects and events (Liszkowski, Carpenter, Henning, Striano, & Tomasello, 2004), but findings also indicate referential intentions in infants' pointing. For instance, in a study by Liszkowski, Carpenter, and Tomasello (2007), in which infants were confronted with a recipient positively emoting to a wrong target, they persisted in their communicative effort until the recipient had correctly identified the event of interest. Shwe and Markman (1997) found infants to correct misunderstandings even after successfully obtaining the desired object, demonstrating that it plays a pivotal role for infants that the referent of their request is properly understood (see also Grosse et al., 2010). Moreover, 12 month old infants seem capable to request absent objects by pointing to the empty place that previously held these objects (Liszkowski, Schäfer, Carpenter, & Tomasello, 2009).

Like the infants in my study, the apes' positioning as well as their production of auditory signals and visual gestures on the other side was foremost driven by the reward location. Unlike infants, however, the reward location also influenced apes' signaling on the experimenter's and they exhibited a predominant preference to gesture visually at the reward location even though the reward itself was hidden under opaque cups (i.e., not visible as for infants). This result is in line with the findings of van der Goot et al. (2014) and Leavens et al. (2015). Van der Goot et al. (2014) showed that chimpanzees always approached the desired item as close as possible before signaling their request, whereas the 12 month old infants continued to point from the distance even when they could have retrieved the reward themselves. However, in their study, experimenter and reward were in the same location. Likewise, in the current study, the apes in the TS condition almost exclusively signaled on the side with the reward (and the experimenter). Leavens et al. (2015) found no preference within their sample of chimpanzees to signal in close proximity to the reward in a setting where the experimenter and the reward were in different locations, while I found such a preference in the TD condition. This might be due to differences in the coding protocols across the two studies, since I coded and compared participants' positioning in relation to the middle line that split the experimental area in half (with experimenter and reward being positioned equally distant from the middle). However, Leavens et al. (2015) compared signals produced in close proximity of the reward to the summed signals produced close to the experimenter and anywhere else in-between those two extreme positions.

Like infants, apes did not increase the frequency of their auditory signals when the experimenter was turned away, but instead exhibited a reversed trend to produce more auditory signals when the experimenter was attentive (turning significant when the ape sample is restricted to the two *Pan* species). This result is in line with others implying that apes do not primarily employ their auditory signals to attract the experimenter's attention (Liebal, Pika, Call, et al., 2004; J. L. Russell et al., 2005; Tempelmann et al., 2011; Tomasello et al., 1994). Nevertheless, like infants, apes auditory signals were less affected by the experimenter's orientation than their visual gestures.

Apes adapted the production of their visual gesturing on the experimenter's side to the experimenter's attentional state. However, unlike infants, the frequency of their visual gestures on the experimenter's side was also strongly affected by the reward location. This was due to apes preferentially gesturing in proximity to the reward, even though this meant they would not be seen when the experimenter was positioned separate from the reward (note however that the two *Pan* species seemed to be less strongly affected by the reward location and more attuned to the experimenter's orientation than the other ape species). Considering the target of the apes' pointing—being positioned in the experimenter's line of sight, apes almost exclusively pointed towards the experimenter. The few pointing gestures directed to the other side occurred foremost from a position in-between sides and were solely driven by the reward location. Crucially, the number of pointing gestures directed towards the other side was not affected by the experimenter's attentional state, suggesting that their pointing did not constitute a deliberate communicative effort to inform the experimenter about the location of the reward. The absence of statistical significance here might be due to a lack of sample size and thus statistical power—applying exactly the same tests to human infants, I found that they pointed marginally more often to the other side when the experimenter was attentive, even though they were less in number (24 infants vs. 32 apes), and trials lasted 10 s less for infants than for apes. Thus, the finding that the apes' pointing to the other side remained unaffected by the experimenter's attentional state seems to indicate that their pointing did not serve the goal to redirect the experimenter's attention (either due to a motivational or cognitive lack).

Yet, the apes might have tried to indicate the reward location by other means. As Menzel (1973) suggested inconspicuous body pointing as a possible mechanism for referential communication in chimpanzees, I also analysed the number of switches between sides. Indeed, participants adapted their switches towards the other side in accordance to the reward location when the experimenter was attentive, but not when he was facing away. However, although participants switched more often to the other side in the TD condition than in the TS condition, they did not switch there less often when the experimenter was inattentive (i.e., in the AD condition). Therefore, it seems unlikely that the switches to the other side constituted a deliberate attempt to communicate about the reward location. However, referential communication via locomotion, as suggested by Menzel (1973), might be more suited for longer distances. Thus, with the distance between the two locations being only about 1.5 m, my experimental set-up might have been inadequate to elicit such communicative behaviour. Finally, the apes might have employed more subtle cues that I did not identify as a means of (referential) communication, such as body postures directed towards the reward or gaze alternation between the reward and the experimenter.

Their pointing gestures, however, were not examples of triadic communication, since unlike infants, who apparently pointed to direct the experimenter's attention to the reward location, apes pointed imperatively to receive food. One potential explanation for this discrepancy between human infants and apes might be the differences in the experimental procedures; that the reward was hidden from the apes' sight, whereas it was visible for infants. Yet, it seems unlikely that this prevented apes from engaging in triadic pointing. Apes clearly remembered the whereabouts of the hidden reward, and I consequently found an location effect on the production as well as the direction of their pointing. What differentiated their communication from that of infants was rather the fact that the experimenter's orientation had no effect on the apes' pointing to the other side. Making the reward visible for apes would have, rather, reinforced the (already prepotent) influence of location and not the other way around. Another difference in the experimental procedure was that infants were tested in a more playful setting than the apes, to keep the incentive to request for both species as strong as possible (as the apes were more motivated to request food than toys). The playful situation might have led infants to be more attuned to the attentional states of the experimenter (although E_1 only adopted a supporting role in the game). However, this is not supported by the GLMM analyses, which did not reveal a differential effect of orientation on infants and apes for any measure except for their pointing to the other side (post hoc tests for the only species x orientation interaction indicated no effects of orientation on the number of auditory gestures on the other side for both species). Thus, it seems unlikely that apes' failure to engage in triadic pointing was due to them being generally less attuned to the experimenter's orientation than infants.

Instead, my results are in line with other studies casting doubt on whether apes point with referential intentions (e.g., Kirchhofer, Zimmermann, Kaminski, & Tomasello, 2012; Tempelmann, Kaminski, & Liebal, 2013). Most notably in this regard, apes fail to comprehend declarative pointing (as referring to hidden food) in the object-choice task. This can be most likely explained by their cognitive restrictions and not the cooperative nature of the task, as shown by a recent study demonstrating the ape's failure to use pointing gestures even in competitive situations (Tempelmann et al., 2013). Furthermore, although apes point imperatively, they seem to not comprehend imperative requests (Kirchhofer et al., 2012). Hopkins, Russell, McIntyre, and Leavens (2013) recently challenged the latter claim by demonstrating that chimpanzees successfully identified the one tube (amongst three) through which they should deliver a requested item based on the experimenter's pointing cue. However, contrary to the task of Kirchhofer et al., where participants were required to return a distant referent, in their task the pointing occurred in close proximity to the target tube (in a distance of 5–10 cm). Thus, it might be that the apes in the study of Hopkins et al. (2013) understood the human's request, but were just using the tube closest to the human's hand to barter the desired object.

As several studies have demonstrated, apes understand the actions of others in terms of intentional motives (Call et al., 2004) and differentiate between attentive and inattentive individuals in communicative as well as competitive situations (e.g., Melis et al., 2006; Tempelmann et al., 2011). Further, chimpanzees can keep track of what others have and have not seen in the past (Hare et al., 2001; Kaminski et al., 2008) and exhibit an implicit sensitivity to the false beliefs of others (Krupenye et al., 2016). Thus, to some extent, apes assign somewhat abstract mental concepts to others to explain and predict their actions.

However, assigning mental states is not necessarily an all-or-nothing affair. Conceptualizing attention as a dynamic mental state that is modifiable and directable might be more challenging than understanding attention as something that can just be either present or absent (see Gómez, 2005 for a similar argument). The latter concept might be sufficiently flexible to predict whether others will react in various cooperative as well as competitive situations, and even enable inferences about whether others are knowledgeable (i.e., have attended) or ignorant (i.e., have not attended), as well as (implicit) knowledge about where others' have last spotted an item (leading to true and false beliefs about entity locations; see Krupenye et al., 2016). However, if it comes to directing other's attention to external objects and events such a concept seems to fail. This would also explain why apes primarily employ their attention-getting signals to draw attention to themselves, rather than using them to specifically draw attention to their visual gestures (Liebal, Call, et al., 2004). If given the chance to do so, they rather maneuver into the recipient's line of sight (Liebal, Pika, Call, et al., 2004). Considering these findings, it seems not surprising that the only systematic observation of ape pointing in natural settings so far—a foot pointing gesture employed by female bonobos to solicit the recipient for genital-genital rubbing—was directed to the sender herself (Douglas & Moscovice, 2015).

Nevertheless, apes are not genetically restricted to such a simplistic concept of attention, as home reared and language-trained apes have been reported to produce and comprehend declarative pointing (reviewed in Leavens & Bard, 2011). While institutionalized apes facing physical restriction might spontaneously acquire the pointing gesture as a means to manipulate human caretakers to gain access to desirable but otherwise out-of-reach objects, the social environment of human infants is vastly different from the one that apes usually encounter in captivity. The socially enriched circumstances (e.g., by extended episodes of joint engagement initiated by human caretakers), under which human infants and language-trained apes are fostered, might contribute to an enhanced understanding of and a higher sensitivity to attentional (as well as other mental) states and thus lead to more sophisticated communicative strategies (Leavens et al., 2015). Furthermore, although the experimental conditions were designed as similar as possible, requesting from others is certainly a more commonplace experience for human infants and language-trained apes than standard-reared captive apes. Therefore, to investigate the performance of enculturated apes with a more rigorously controlled experimental paradigm to that of the current study might be an interesting venue for future research.

4. Study 3

Two FB Tasks With Reduced Requirements for Inhibitory Control

Recent studies have demonstrated that young infants and great apes are sensitive to others' belief states. Nevertheless, they fail in more explicit tests of false belief understanding. Some have argued for humans that the lack of inhibitory control might be responsible for the failures of younger infants in explicit false belief tasks. Likewise, a lack of inhibitory control might have been precluding chimpanzees' implicit capacities to compute others beliefs in all studies to date. Therefore, my goal in the present study was to devise a false belief task with reduced requirements for executive function. To this end, I employed the basic paradigm from Kaminski et al. (2008) in which chimpanzees competed in a turn-taking game with a conspecific for a hidden reward. However, the paradigm was modified by ensuring that participants (1) did not have any preference amongst alternative choices ('no preference' task) or (2) did not have any knowledge of the location of the preferred reward ('no knowledge' task). To be better able to relate the results to human false belief understanding, 5.5 year old preschool children were tested in the same paradigm as the chimpanzees.

4.1 Introduction

Chimpanzees, like humans, have a flexible understanding of some psychological states in others. They are able to assess others' goals and intentions (e.g., Call et al., 2004) and understand what others see (e.g., Bräuer et al., 2007; Hostetter et al., 2007) and know (Hare et al., 2001; Kaminski et al., 2008). A recent study discovered that great apes are also sensitive to reality incongruent belief states (i.e., false beliefs) of others (Krupenye et al., 2016). In this study Krupenye et al. (2016) investigated great apes' anticipatory looks in a false belief situation. In the familiarization phase, participants observed that a human (actor) who witnessed the hiding of a desired goal object would search for it in one of two existing hiding places. In the false belief situation, the attentive human either left the experimental area before or after the object was transferred to the alternative hiding place. Finally (and still in the human's absence), the object was completely removed from the scenery. When the human returned, participants expected him to search for the object where he last had spotted the object (as indicated by their anticipatory looking), suggesting that they were sensitive to his false belief regarding the location of the object. Other than this intriguing example, to date great apes have failed in all tasks that required an explicit understanding of beliefs (Call & Tomasello, 1999; Kaminski et al., 2008; Krachun et al., 2009, 2010; O'Connell & Dunbar, 2003).

Call and Tomasello (1999) were the first to devise an explicit non-verbal false belief task for apes (and children). In their study, a reward was hidden beneath one of two opaque containers by a human baiter. The hiding took place unseen by the participant but in sight of a helpful human ('the communicator'). The communicator then indicated the reward location by placing a marker on top of the respective container. In the critical false belief situation of the task, the communicator left the room while the baiter switched the positions of the cups. Most of the 5 year old children acknowledged the returning communicator's false belief and correctly chose the unmarked cup. Most of the 4 year old children and the apes on the other hand failed to do so.

As some have found that primates perform better in social cognitive tasks when these are embedded within a competitive situation (e.g., Hare & Tomasello, 2004) Krachun et al. (2009) modified the basic paradigm of Call and Tomasello (1999) so that the communicator was replaced by a (human) competitor who was (unsuccessfully) reaching for the container that she believed held the reward (i.e., the empty container in false belief trials). Again, 5 year old children mastered the task whereas apes failed. Krachun et al. (2010) also devised a non-verbal change-of-contents task in a neutral context. In this study, a human baiter first filled an opaque container with one of two possible reward types and then subsequently moved the container to a location corresponding to the reward type (i.e., containers holding reward type A were always moved to location A and containers holding reward type B were always moved to location B). In the critical false belief test situation, a second human replaced the original reward with the other reward type while the baiter was absent (i.e., in-between baiting and placement of the container to its final location). As in the cooperative and the competitive paradigms, apes failed to acknowledge the baiter's false belief and expected her to place the container appropriate to its actual content.

Employing another competitive paradigm, Kaminski et al. (2008) found that chimpanzees differentiated between knowledgeable and ignorant competitors but still failed to attribute false beliefs. In this paradigm, the chimpanzees took turns with a conspecific competitor to choose from opaque cups which contained hidden rewards. In the knowledge-ignorance task, two reward pieces were hidden beneath two out of the three cups. Whereas the baiting of one reward was observed by both the competitor and the participant, the baiting of the second reward was seen by the participant only. Subsequently, either the competitor or the participant chose a cup. If competitors chose first, the participants preferentially selected the cup that contained the reward unseen by the competitor (whereas having no preference for either cup when they chose first themselves); indicating that they were keeping track of what the competitor knew (in the sense of what they had or had not seen). In the false belief task, one piece of preferred reward was placed beneath one of two cups accessible to the participant and the competitor, whereas the second piece of a less attractive reward was placed beneath a cup only accessible to the participant. Following this baiting (which was always visible to both the competitor and the participant), the experimenter manipulated the cups either by switching their positions or lifting them and putting them back to their original locations. This manipulation was either seen or unseen by the competitor. While the chimpanzees chose the preferred reward more often when the competitor had not observed the manipulation, it did not make a difference whether the cups were lifted (leading to a true competitor belief) or switched (leading to a false competitor belief), indicating that they failed to acknowledge the competitor's belief.

On the basis of the studies above, it can be ruled out that chimpanzees' failure to acknowledge others' false beliefs is due to cooperative task demands or due to the use of interspecific agents. However, all studies to date required the chimpanzees to inhibit a prepotent response which either resulted from: cues making one alternative more salient than the other (Call & Tomasello, 1999; Krachun et al., 2009); conflicting own true beliefs (Krachun et al., 2010), or having an intrinsic preference for one of the alternatives (Kaminski et al., 2008). All of these arguably tax participants' executive functioning. Studies with human infants indicate that executive function is linked to perspective selection and false belief understanding and that performance in tasks taxing inhibitory control correlates with performance in false belief tasks (e.g., Qureshi et al., 2010; Rakoczy, 2010; Sabbagh et al., 2006). In line with this, several studies taking implicit measurements have demonstrated that infants exhibit some sensitivity to the belief states of others (reviewed in Baillargeon et al., 2010) long before they pass classic verbal belief tasks (reviewed in Wellman et al., 2001).

For instance, it has been found that 15-month-olds look longer at an agent's searching if she does not search for an desired object in the location where she last saw it hidden (Onishi & Baillargeon, 2005). Likewise, infants engage in anticipatory looking such that they look first towards the location where the agent last saw an object even though the object had been displaced in the agent's absence (Clements & Perner, 1994; He, Bolz, & Baillargeon, 2012; Senju, Southgate, Snape, Leonard, & Csibra, 2011; V. Southgate, Senju, & Csibra, 2007). Also in studies employing helping paradigms, infants have been shown to act in accordance with an agent's (false) belief (D. Buttelmann, Carpenter, & Tomasello, 2009; D. Buttelmann, Over, Carpenter, & Tomasello, 2014; F. Buttelmann, Suhrke, & Buttelmann, 2015; Knudsen & Liszkowski, 2012a, 2012b; Victoria Southgate, Chevallier, & Csibra, 2010). This discrepancy between early belief sensitivity and failure in classic verbal false belief tasks has led some to postulate the existence of an early module for belief detection which matures to an adult-like false belief understanding through the development of executive functioning (e.g., Baillargeon et al., 2010; Leslie et al., 2004). According to this account infants' failure in verbal false belief tasks is due to performance problems in suppressing their own true belief.

Likewise, it might be that apes' failure in the false belief tasks mentioned above is due to a lack in inhibitory control. In this regard, it is noteworthy that younger children (who are also known to be sensitive to false belief states), who were investigated through the same non-verbal false belief paradigms as used for the apes, performed similar to the ape participants, and that only older children performed better. Further, some studies have found that chimpanzees perform in various tasks related to inhibitory control similarly to 3-year-olds, but less skillfully than 6-year-olds (Herrmann, Misch, Hernandez-Lloreda, & Tomasello, 2015; Herrmann & Tomasello, 2015; cf. Rosati, Stevens, Hare, & Hauser, 2007; Vlamings, Hare, & Call, 2010).

To find out if chimpanzees' false belief understanding has been precluded by their lack of inhibitory control, my goal in the current study was to devise a false belief task with reduced requirements for executive function. I attempted to achieve this by modifying the task from Kaminski et al. (2008), such that either (1) participants did not have any preference amongst the alternative choices ('no preference' study) or (2) they did not have any knowledge of the location of the preferred reward ('no knowledge' study). In the critical test situation of the 'no preference' study, the competitor and the participant observed how one of two identical opaque cups was baited with a high quantity of reward, whereas the other cup was baited with a low quantity of reward. While the competitor's view was blocked, the experimenter either removed reward from the high quantity cup or added reward to the low quantity cup until both cups finally held the same amount of reward. Thus, while both cups were equally attractive to the participant, the competitor falsely believed one cup to hold a higher quantity of reward. In the critical test situation of the 'no knowledge' study, the competitor observed how one of two identical opaque cups was baited with a preferred reward but did not see that the experimenter subsequently switched the position of the cups. As in the tasks of Call and Tomasello (1999) and Krachun et al. (2009), participants did not observe the baiting of the cups but saw the switching of the cups, whereas the competitor had no visual access during this manipulation. However, unlike Call and Tomasello (1999) and Krachun et al. (2009), to further reduce the inhibitory requirement of the task at hand, no additional cues highlighting one of the cups were given.

If apes understanding of others' false beliefs has been precluded by a lack of inhibitory control in previous studies I expect the chimpanzees to succeed in the two novel tasks. However, if apes' failure to demonstrate and understanding of false beliefs in previous tasks was due to a conceptual lack, they should still fail in the two novel tasks. To be better able to relate the results to human false belief understanding, 5.5 year old preschool children were tested in the same paradigms as the chimpanzees.

4.2 Experiment 1: No Preference

The goal of the first experiment was to design a non-verbal false belief task with reduced inhibitory demands. To accomplish this the basic paradigm from Kaminski et al. (2008) was modified so that all alternative choices were equally attractive for participants, while attractiveness was varied to their competitors through their (false) beliefs about the contents of the different alternative choices.

4.2.1 Methods

Participants. Twelve chimpanzees (five females, seven males) socially housed at the Ngamba Island Chimpanzee Sanctuary, Uganda, with the mean age of 12.8 years (*SD* = 1.5 y; range: 10–15 y) participated in the study (see Appendix C.1 for more detailed information). All chimpanzees came to the sanctuary as orphans due to illegal trade in bushmeat. They were reared by humans together with conspecifics. During the day they spent their time in a natural forest habitat on the island. All participants were tested individually and were neither deprived of food or water. Further, 12 human preschool children (7 females, 5 males) from a kindergarten in a medium-sized German city with the mean age of 5.52 years (*SD* = 0.28 y, range: 5.04–5.88 y) were recruited to participate in the study. All participants were tested individually and were ignorant about the purpose of the study.

Experimental set-up. See Fig. 9 for a schematic picture of the set-up (for exact measurements, see Appendix C.2). Set-up and procedure were adapted from Kaminski et al. (2008). The general method was a game in which the participant and a conspecific competitor took turns choosing from two opaque cups that contained hidden rewards. Both individuals sat opposite to each other, with a sliding platform between them on which the two cups were positioned. The experimenter sat between participant and competitor and was responsible for the baiting of the cups with reward, as well as the moving of the sliding platform back-and-forth between both individuals. The task began with a hiding event, during which the two cups were baited with different quantities of rewards.

The same adult male chimpanzee (Asega, approximate age 13 years) served as a competitor *stooge* for the chimpanzee participants in all sessions, with the exception of two; where due to lack of motivation to participate, Asega was replaced by another male (Mawa, approximate age 15 years). Chimpanzees received either banana or apple pieces as reward (all cut into same-sized pieces). The same adult female human served as competitor stooge for all preschool children participants. Children received sweets (M&M's®) as rewards (only same-coloured M&M's were used within a given trial).

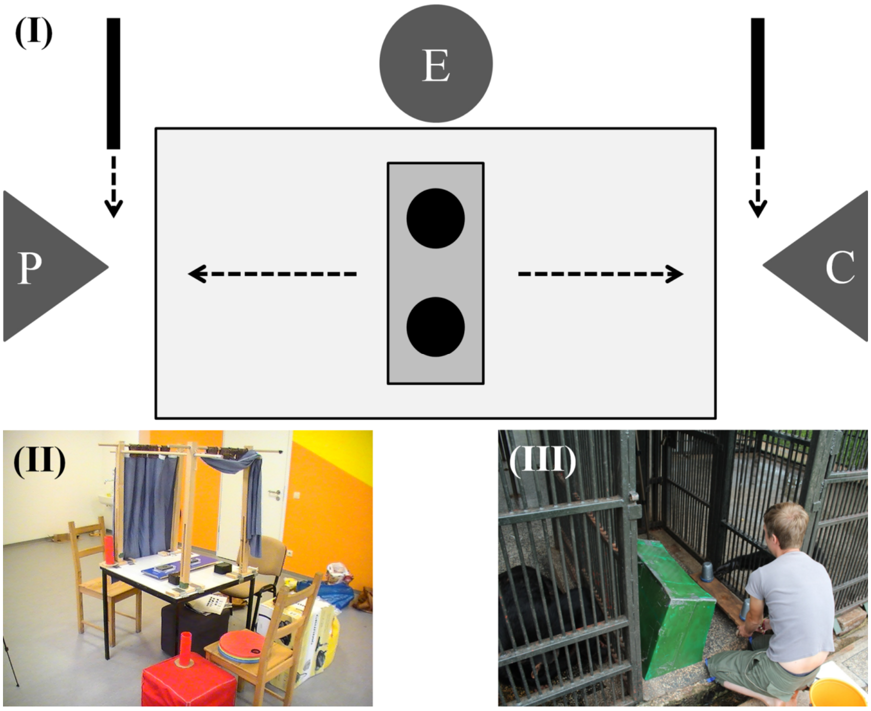

Figure 9. Experimental set-up. (I) Schematic drawing with the two cups on top of the sliding platform in the middle, participant (P) on the left side, competitor (C) on the right side and experimenter (E) on top; participant's and competitor's view on the scenery could be blocked with blinds (black bars to the left and right of E) to occlude specific events as the baiting and the manipulation of the cups and the competitor's choice of cups; (II) set-up for preschool children; (III) set-up for chimpanzees

Warm-up trials. In order to familiarize participants with the game, they received several blocks of warm-up trials prior to the actual testing. In warm-up trials, the experimenter baited, in full view of the participant and the competitor, one cup with one piece of reward (low quantity, henceforth LQ) and the other cup with three pieces of reward (high quantity, henceforth HQ). Then either the participant or the competitor indicated their choice by pointing in full view of the other. After the experimenter delivered the selected reward and placed the cup back to its original position, the other individual was allowed to choose. The experimenter continued to move the cups back and forth between the two individuals until both cups were empty.

Chimpanzees received blocks of six warm-up trials. Each cup was served three times as container for the HQ reward and three times as container for the LQ reward. In half of the trials the competitor chose first, in the other half of the trials the participant chose first. Trials were counterbalanced such that participants received the HQ reward at least once from each cup. Once participants chose the correct cup (i.e., the LQ cup when the competitor made the first choice and the HQ cup if they themselves chose first) at least five times, the actual testing started. All participants reached this critical criterion within the first block of warm-up trials.

Children received blocks of three warm-up trials. HQ and LQ rewards were pseudo-randomly allocated such that each cup served at least once as HQ cup. In two trials, the competitor made the first choice, in one trial, participants were the first to choose. Participants were required to successfully choose the correct cup in all three trials to proceed to the actual testing (11 of 12 children reached this criterion within the first block of warm-up trials while one child required two blocks of warm-up trials). Prior to warm-up, children received the following verbal instruction from the experimenter: “You will play a game against C[1] for M&M's. I will hide the M&M's beneath these two cups. When I move the cups to C, C may choose a cup. When I move the cups to you, it's your turn and you may choose a cup. Throughout the game it is not allowed to talk. Thus, both of you indicate the cup that I shall give you by pointing. You will always get all the M&M's hidden beneath a cup. If you point to an empty cup you will receive nothing. Let us practice first."

Experimental trials. The procedure in experimental trials differed in several aspects from the one in warm-up trials. Subsequently to the initial baiting of the two cups as LQ and HQ ('baiting phase'), the experimenter manipulated the content of either the LQ cup or the HQ cup by adding or removing reward respectively ('manipulation phase') such that both cups contained the same amount of reward in the end (i.e., either reward was added to the LQ cup resulting in both cups finally containing three pieces of reward or reward was removed from the HQ cup resulting in both cups finally containing one piece of reward). While participants always observed hiding as well as manipulation, I systematically varied which of the two phases competitors did and did not see depending on the experimental condition (see Fig. 10 and Fig. 11).

(1) ***Uninformed (UI).*** Competitors observed neither the baiting nor the manipulation and were hence ignorant about the contents of both cups. Competitors in the UI condition should choose randomly between LQ and HQ cups. Consequently, participants exploiting the competitor's belief should neither prefer the LQ nor the HQ cup, regardless of manipulation type. Participants engaging in a perceptual access strategy might prefer to choose the cup that was manipulated in concealment (i.e., the LQ cup if reward was added and the HQ cup if reward was removed).

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[1] competitor name

(2) ***Partially informed (PI).*** Competitors' line of sight was blocked during baiting, whereas they were able to see the manipulation phase. Thus, competitors knew the content of the manipulated cup and remained uninformed about the content of the second cup. Competitors in the PI condition should choose the cup the contents of which they saw (i.e., the LQ cup if reward was added and the HQ cup if reward was removed). Therefore, participants should preferentially choose the HQ cup if reward was added and the LQ cup if reward was removed regardless of whether they exploited beliefs or were following a perceptual access strategy.

(3) ***Misinformed (MI).*** Competitors observed the baiting, whereas their line of sight was blocked during the manipulation phase, leading competitors to the false belief that the HQ cup still held more reward than the LQ cup, whereas in fact both held same amount of reward. Thus, in the MI conditions competitors should choose the HQ cup. Consequently, participants exploiting the competitor's belief should preferentially choose the LQ cup irrespective of manipulation type. Participants operating on the basis of a perceptual access strategy should preferentially choose the cup that was manipulated in concealment (i.e., the LQ cup if reward was added and the HQ cup if reward was removed).

(4) ***Fully informed (FI).*** Competitors observed the baiting as well as the manipulation and thus knew the contents of the LQ cup as well as the HQ cup (i.e., that both held the same amount of reward). Therefore, in the FI condition, competitors should choose randomly between the LQ and HQ cup. Consequently, participants engaging in belief reasoning should neither prefer the LQ nor the HQ cup, regardless of manipulation type. Participants engaging in a perceptual access strategy might prefer to choose the cup that was not revealed during manipulation (i.e., the HQ cup if reward was added and the LQ cup if reward was removed).

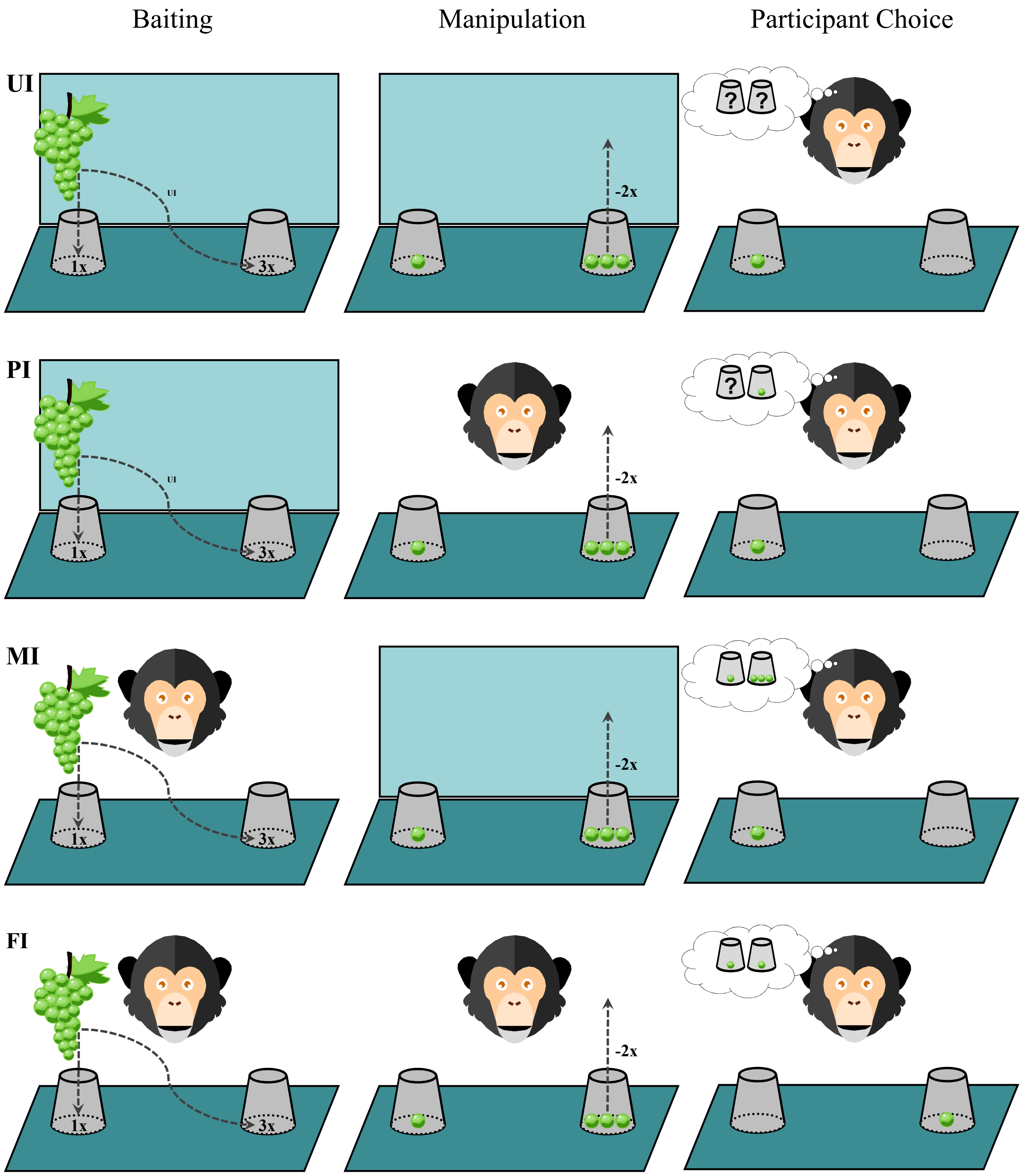

Figure 10. Test situation from participants' perspective before the initial baiting of the two cups ('Baiting'), removal of reward ('Manipulation'), and after competitor has made a choice ('Participant Choice') for all experimental conditions (UI: uninformed, PI: partially informed; MI: misinformed, FI: fully informed); face visible: competitor observes event; face invisible: competitor's line of sight is blocked; thought bubble: information that the competitor based his choice on.

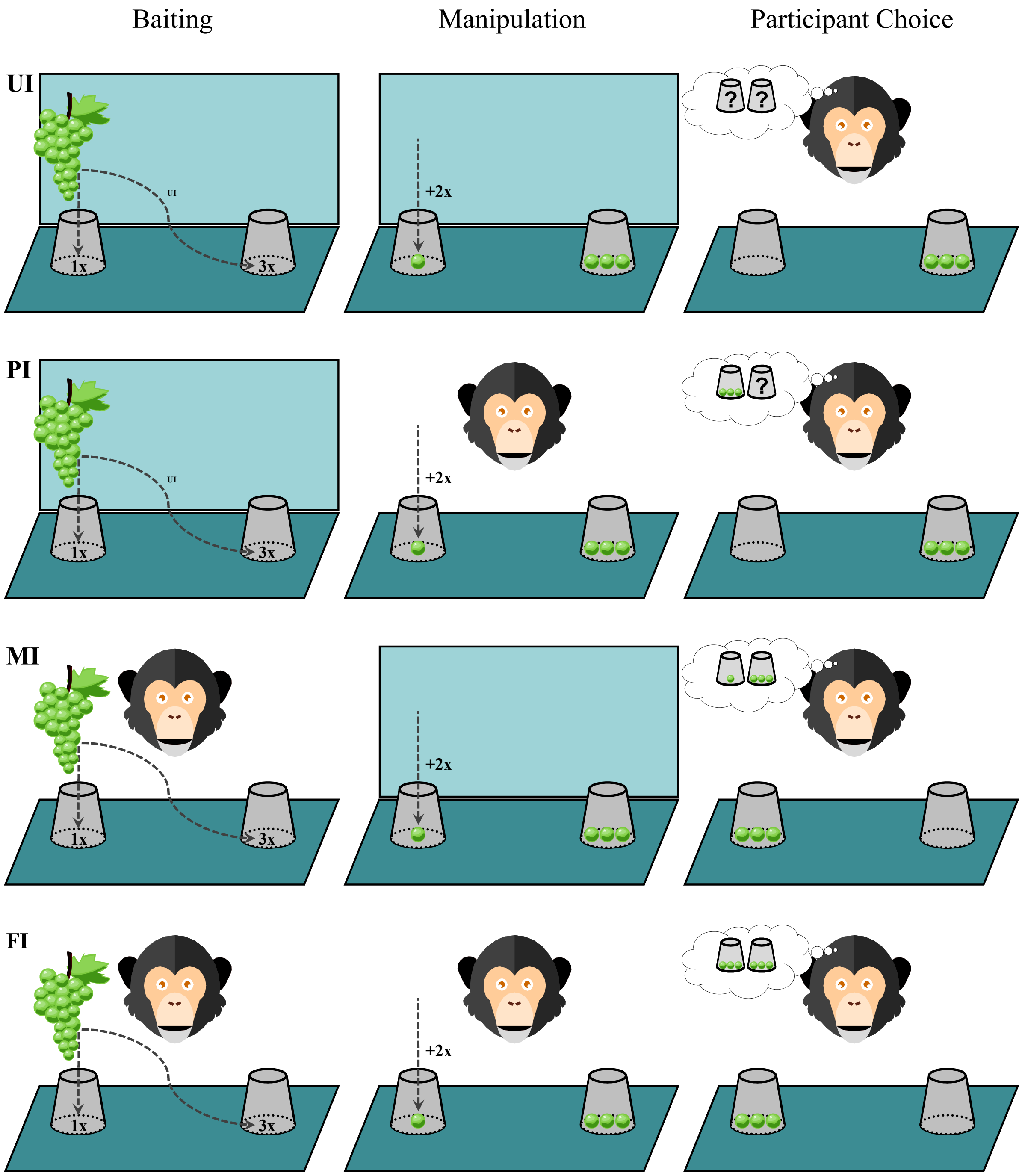

Figure 11. Test situation from participants' perspective before the initial baiting of the two cups ('Baiting'), addition of reward ('Manipulation'), and after competitor has made a choice ('Participant Choice') for all experimental conditions (UI: uninformed, PI: partially informed; MI: misinformed, FI: fully informed); face visible: competitor observes event; face invisible: competitor's line of sight is blocked; thought bubble: information that the competitor based his choice on.

Contrary to warm-up trials, competitors always chose first, while the participants' line of sight was blocked. The human competitor was instructed to always point in the middle between the two cups (to minimize the risk of inadvertently giving away discriminating cues to the participants) while the chimpanzee competitor was pointing freely. Competitors always received a cup predetermined according to the theoretical prediction of an ideal choice (see above) regardless of the competitor's actual choice. In the conditions where competitors should choose randomly (i.e., UI and FI), the predetermined choice was counterbalanced such that competitors received the LQ and the HQ cup equally often. The agreement between the actual choice of the chimpanzee competitor and the predetermined choice was at chance levels for UI (56%, Cohen's $\kappa = .12$, $N = 141$, p = .149) and FI (53%, $\kappa = .06$, $N = 142$, $p = .486$). Agreement for PI was 82% ($\kappa = .65$, $N = 142$, $p < .001$) and 90% for FI ($\kappa = .82$, $N = 143$, $p < .001$).

As participants did not see the competitor's choice, they never knew which of the two cups was empty and which one still contained reward when choosing themselves. To succeed in the task, they had to utilize the available information on what the competitor had and had not seen. Participants exploiting the competitor's belief should exhibit the lowest overall rate of HQ choice in the MI condition as they should avoid the HQ cup for both manipulation types. In the PI condition, they should avoid the cup that was revealed to the competitor during manipulation (i.e., HQ when reward was removed and LQ if reward was added) resulting in a HQ choice rate of 0.5 averaged over both manipulation types. Likewise, participants should choose the HQ in half of the trials in UI and FI, however, without showing any differences across manipulation types. If participants were following a perceptual access strategy, they should have a preference for the manipulated container when the manipulation was not visible to the competitor (i.e., in UI and MI). In contrast, they should avoid the manipulated container when the competitor had observed the manipulation (i.e., in PI and FI). Thus, in the PI and FI conditions, participants should exhibit a higher rate of HQ choice when reward was added than when reward was removed, whereas they should have exhibited the reverse pattern in the UI and MI conditions.

In half of the trials two pieces of reward were removed from the HQ cup (resulting in one reward piece beneath each cup), in the other half of the trials two pieces of reward were added to the LQ cup (resulting in three reward pieces beneath each cup). Condition, type of manipulation and position of cups were pseudo-randomized such that neither of these were the same in more than two trials in a row. Chimpanzees received a total of 48 trials, split up into two sessions of 24 trials each on two consecutive days (i.e., 12 trials per condition—six trials per condition in which reward was added and six trials per condition in which reward was removed). Each child received a total of 32 trials, split up into two sessions of 16 trials each on two consecutive days (i.e., eight trials per condition—four trials per condition in which reward was added and four trials per condition in which reward was removed).

Coding and analysis. Trials were live coded and recorded by digital camcorders from different angles. Scores were finalized from the video files. I scored whether participants chose the HQ or the LQ cup. A second observer scored 22% of the trials to assess the inter-observer reliability of the participant choices. Agreement between coders was excellent (Cohen's $\kappa = .99$).

Wilcoxon signed-ranks tests were used to compare the average ratio of HQ choice in each condition against chance levels (i.e., 0.5) and to compare the ratio of HQ choice across manipulation types within conditions. Further a Generalized Linear Mixed Model (GLMM) analysis was conducted to assess the effects of the two predictor variables condition and manipulation type on the ratio of HQ choice. Full models included the two main variables condition and manipulation type, their interaction, as well as sex, trial order, and participant random effects as fixed factors. All analyses were conducted using the statistic software R (R Core Team, 2014). Cup choice was modeled as binomial distribution via the lme4-package (D. Bates et al., 2015).

4.2.2 Results

When reward was added, the chimpanzees chose the HQ cup significantly less often than expected by chance in the PI condition (Wilcoxon signed-ranks test against 0.5; $T_+ = 52.0$, $N = 10$, $p = .008$; see Fig. 12), whereas the ratio of HQ cup choice did not differ significantly from chance in any of the other conditions (Wilcoxon signed-ranks test against 0.5; UI: $T_+ = 12.0$, $N = 5$, $p = .250$; MI: $T_+ = 16.0$, $N = 7$, $p = .859$; FI: $T_+ = 14.0$, $N = 6$, $p = .594$). When reward was removed, the chimpanzees chose the HQ cup significantly more often than expected by chance in the MI condition (Wilcoxon signed-ranks test against 0.5; $T_+ = 45.0$, $N = 9$, $p = .004$), whereas there was no difference in the ratio of HQ cup choice in any of the other conditions (Wilcoxon signed-ranks test against 0.5; UI: $T_+ = 22.0$, $N = 7$, $p = .219$; PI: $T_+ = 48.5$, $N = 11$, $p = .193$; FI: $T_+ = 35.0$, $N = 9$, $p = .160$). Comparing the ratio of HQ cup choice across manipulation types revealed that chimpanzees in the PI condition chose the HQ cup more often when reward was removed (Wilcoxon signed-ranks test; $T_+ = 42.5$, $N = 9$, $p = .016$) whereas no differences was found between manipulation types in any of the other conditions (UI: $T_+ = 21.0$, $N = 7$, $p = .281$; MI: $T_+ = 25.0$, $N = 8$, $p = .320$; FI: $T_+ = 35.5$, $N = 9$, $p = .148$). Further, a GLMM revealed a significant overall effect of the variables on the ratio of HQ cup choice ($\chi^2 = 14.38$, $df = 7$, $p = .045$; see Appendix C.3). This was due to chimpanzees choosing the HQ cup more often when reward was removed than when reward was added (main effect of manipulation type: -0.37 ± 0.17, $p = .030$). This effect was independent of condition ($\chi^2 = 7.45$, $df = 3$, $p = .059$).

The ratio of childrens' HQ cup choice did not differ significantly from chance in any of the conditions, either when reward was added (Wilcoxon signed-ranks test against 0.5; UI: $T_+ = 22.5$, $N = 8$, $p = .727$; PI: $T_+ = 16.0$, $N = 7$, $p = 1$; MI: $T_+ = 7.5$, $N = 4$, $p = .625$; FI: $T_+ = 24.5$, $N = 9$, $p = .972$) or when reward was removed (Wilcoxon signed-ranks test against 0.5; UI: $T_+ = 15.0$, $N = 5$, $p = .063$; PI: $T_+ = 25.5$, $N = 9$, $p = .828$; MI: $T_+ = 25.0$, $N = 9$, $p = 1$; FI:

$T_+ = 26.0$, $N = 9$, $p = .727$). Neither were there any differences across manipulation types (Wilcoxon signed-ranks test; UI: $T_+ = 24.0$, $N = 8$, $p = .563$; PI: $T_+ = 18.5$, $N = 8$, $p = 1$; MI: $T_+ = 12.0$, $N = 6$, $p = 1$; FI: $T_+ = 20.5$, $N = 8$, $p = .781$). Further, the GLMM did not indicate an overall effect of the test factors on the ratio of HQ cup choice ($\chi^2 = 2.63$, $df = 7$, $p = .917$).

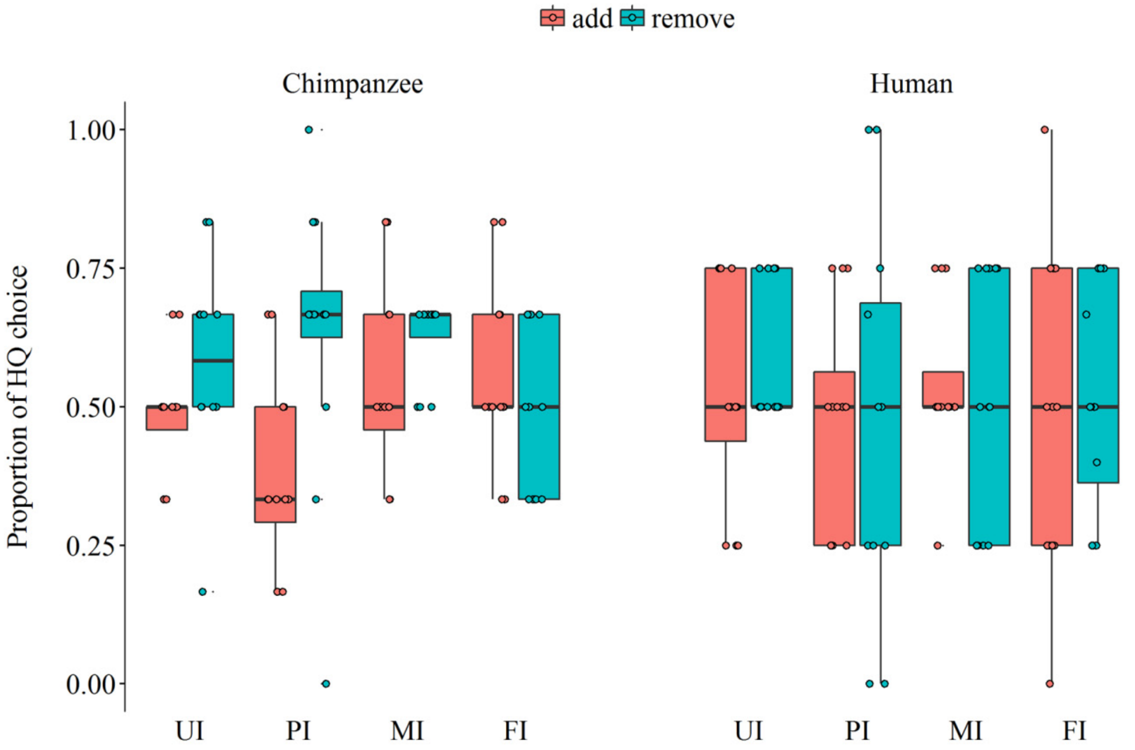

Figure 12. Average ratio of HQ cup choice of chimpanzees (left) and human children (right) across manipulation types (red: add, blue: remove) and conditions (UI: uninformed, PI: partially informed, MI: misinformed, FI: fully informed); box length = interquartile range; whisker length = 1.5 x interquartile length.

4.2.3 Discussion

The chimpanzees in the PI condition chose the HQ cup more frequently when reward was removed than when reward was added. In the MI condition they chose the HQ cup significantly more often than expected by chance. Further they exhibited a general preference to choose the cup that was manipulated by the experimenter. This pattern does neither fit the prediction of a perceptual access strategy nor does it fit to a performance exploiting the competitor’s belief. It appears as if the chimpanzees did not account at all for the competitor's informational state. Rather their choices seemed to be driven by a tendency to choose the cup that was most recently revealed. Unlike the chimpanzees, the preschoolers' choice was not driven by a recency effect. Nevertheless, also the children failed to account for what the competitor had and had not seen throughout baiting and manipulation.

Participants' failure to adapt their choices to the competitor in any of the conditions is especially puzzling as chimpanzees have been demonstrated to keep track of what others have seen (e.g., Hare et al., 2001; Kaminski et al., 2008). Likewise, 5.5 year old children fall well into the age range where they are capable of solving explicit false belief tasks (reviewed in Wellman et al., 2001). Further, chimpanzees (including individuals from the very same population and sample tested in the current study) and 5 year old children have been shown to succeed in the same basic paradigm that only slightly deviates from the procedure in the task at hand (Kaminski et al., 2008; Karg et al., 2016; Schmelz et al., 2011, 2013). For instance, the PI condition of the current study parallels the knowledge-ignorance study of Kaminski et al. (2008). In the latter study, competitors observed the baiting of one of three cups but did not see the baiting of the second reward (and the empty cup). Likewise, in the PI condition, competitors saw the contents of one of the cups and remained uninformed about the contents of the second cup. The two main differences between these tasks were that (1) I used two cups instead of three (which should simplify the current task) and (2) my task was about how much reward the cups contained (in contrast to whether or not the cups contained reward) and involved up to six pieces of reward (when reward was added), each of whose positions had to be tracked twice. First participants had to remember the rewards physical position, second they had to keep track where their competitor believed the reward pieces to be. Thus, instead of reducing inhibitory demands this might have lead to higher task demands by increasing the overall cognitive load. As Schneider, Lam, Bayliss, and Dux (2012) have demonstrated implicit theory of mind performance (as indicated by looking times) can be disrupted by increasing the overall cognitive load of the task (e.g., by prompting participants to detect and count audio stimuli in parallel). This could also be a possible explanation for the 5.5-year-olds failure in the task at hand.

4.3 Experiment 2: No Knowledge

The goal of the second experiment was to reduce the inhibitory demands for participants by leaving them uninformed about the location of the reward thereby relieving them of the necessity to suppress their knowledge of reality in a false belief situation. Without having any own knowledge of the exact whereabouts of the reward, participants had to focus on what their competitor had observed. If participants observe a difference between being uninformed and misinformed this should influence their choice behaviour. A misinformed competitor will make a wrong choice, whereas an uninformed competitor might still be right by chance. Thus, participants should feel more confident to retrieve a contested reward when faced with a misinformed, rather than uninformed, competitor. Experiment 2 employed the same basic paradigm of a turn-taking game as experiment 1 with some minor variations.

4.3.1 Methods

Participants. Participants were 12 chimpanzees (see Appendix C.1) and 14 human children. All chimpanzees and 12 of the 14 human children had already participated in experiment 1. Due to a lack of observed motivation to participate in all sessions of experiment 2, two of the original 12 children (male: 5 y, 7 m, 1 d; male: 5 y, 7 m, 26 d) were replaced by two new participants (male: 5 y, 2 m, 30 d; female: 5 y, 3 m, 22 d).

Experimental set-up. The basic setup was the same as in experiment 1 with the following modifications. Additionally to the two cups on the sliding board (henceforth termed ‘main-board’), I introduced a third, stationary cup that was placed distantly from the competitor and only available to participants (henceforth termed ‘opt-out’). The task began with the baiting of the cups on the main-board and the opt-out cup.

For motivational reasons, I alternated between three different chimpanzee competitors—the two competitors from experiment 1 (Asega: 14 sessions; Mawa: 10 sessions) and a newly introduced competitor (Ikura; female, approximate age 16 years: 24 sessions). Participants were always facing the same competitor for all trials with one exception (‘Indi’: Asega as competitor for the first half of trials, Mawa as competitor for the second half). Chimpanzees received either banana or apple as reward (all cut into same-sized pieces).

The same adult female human as in experiment 1 served as competitor stooge for all preschool children participants. Children received sweets (M&M’s®) as rewards (only same-coloured M&M’s were used within a given trial).

Warm-up trials. Prior to the actual testing, participants received several blocks of warm-up trials. In warm-up trials the experimenter baited, in sight of the participant and the competitor, one of the two cups on the main-board with two pieces of reward, and placed one piece of reward under the opt-out cup. Then either the participant or the competitor made their choice in full sight of the other. If one of the two cups on the main-board was chosen, the experimenter delivered the rewards beneath the cup. Instead of placing the cup back at its original position as in experiment 1, the experimenter then removed the chosen cup from ‘play’ (i.e., view). Subsequently, the experimenter moved the remaining cup into the middle of the sliding board before pushing the sliding board to the player on the other side.

Chimpanzees received blocks of six warm-up trials. Each main-board cup remained empty in half of the trials while containing the reward in the other half. In four trials the competitor chose first, in the other two trials the participant chose first. Trials were counterbalanced such that the competitor was first no more than three times in a row, and that each main-board cup was not rewarded more often than three times in a row. If participants chose the correct cup (i.e., the opt-out cup when the competitor made the first choice and the baited main-board cup if they themselves chose first) at least five times, the actual testing started. Ten out of 12 participants reached this critical criterion within the first block of warm-up trials, while two participants received two and three blocks respectively (mean number of trials = 7.5, *SD* = 3.7).

Children received blocks of three warm-up trials. Rewards were pseudo randomly allocated such that each main-board cup served at least once as container for the two reward pieces. In two trials, the competitor made the first choice, in one trial, participants were the first to choose. Participants were required to successfully choose the correct cup in all three trials to proceed to the actual testing. Six out of 12 children reached this criterion in the first block of warm-up trials while the other six achieved the performance criterion within two blocks (mean number of trials = 4.7, *SD* = 1.5). Prior to warm-up, children received the following verbal instruction from the experimenter: "You will play a game against C[2] for M&M's. This time I will always hide two M&M's beneath one of these two cups—either beneath this one [pointing to one of the two cups on the main-board] or beneath this one [pointing to the alternative cup on the main-board]. When I move the cups to C, C may choose a cup. When I move the cups to you, it's your turn, and you may choose a cup. You may also choose this cup [pointing to the opt-out]. C is not allowed to choose this cup. Beneath the cup there is always one M&M. Though one M&M is less than two, it's still better than no M&M at all. Throughout the game it is not allowed to talk. Thus, both of you indicate the cup that I shall give you by pointing. You will always get all the M&M's hidden beneath a cup. If you point to an empty cup you will receive nothing. Let us practice first."

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[2] Competitor name

Experimental trials. The procedure in experimental trials differed slightly from the one in warm-up trials as follows. Subsequently to the initial baiting of the two main-board cups and the opt-out cup ('baiting phase'), the experimenter manipulated the main-board cups by either lifting the cups and placing them back to their original position (lift control trials, see below) or by switching their positions ('manipulation phase'). I systematically varied what information about the baiting of the main-board cups was available to participants. Participants could either freely observe the baiting ('knowledge' type trials) or a small opaque blind occluded their line of sight onto the cups while still allowing them to see the competitor ('ignorance' type trials). Participants always observed the manipulation but never the competitor choosing (both irrespective of the information type of the trial). Further, I systematically varied whether competitors did and did not see baiting and the manipulation according to the following four experimental conditions (see also Fig. 13).

(1) ***Uninformed (UI).*** The competitors observed neither the baiting nor the switching of the cups and were hence ignorant about the contents of both cups. Therefore, competitors should choose randomly between both cups, leaving the reward in half of the trials on average.

(2) ***Partially informed (PI).*** The competitors' line of sight was blocked during baiting but not during the switching of the cups. Since observing the switching without knowing the contents of the cup did not provide any helpful information, competitors should choose randomly between both cups, leaving the reward in half of the trials.

(3) ***Misinformed (MI).*** The competitors observed the baiting, whereas their line of sight was blocked during the switching. Thus, competitors should choose the empty cup, leaving the reward for the participants..

(4) ***Fully informed (FI).*** The competitors observed the baiting as well as the manipulation. Thus, competitors should choose the baited cup leaving no reward for the participant.

Experimental trials were grouped together into sessions of same information type trials. If participants were exploiting the competitor's belief, main-board cup choice should be highest in the MI condition and lowest in the FI condition with the UI and the PI conditions ranging in-between. Participants following a perceptual access strategy should have had exhibited the highest level of main-board cup choice in the UI condition and the lowest level of main-board cup choice in the FI condition with the PI and the MI conditions ranging in-between. Further, I expected participants to perform better if they had no own knowledge of the baiting themselves. In addition to the four experimental conditions, each session also contained two different kinds of control trials:

(5) ***Opt-out control (OC).*** OC trials were introduced to check whether participants remained aware about the newly introduced OC cup as an alternative choice to the cup on the main-board. OC trials were identical to FI trials except that participants were allowed to see the competitor choosing. Each session started with an OC trial. If participants failed in these, they received another round of warm-up blocks until they reached criterion performance again (i.e., 5 out of 6 correct warm-up trials). Re-training occurred in 9% of all sessions for infants and 36 % of all sessions for chimpanzees. All participants finished re-training within 1 block of warm-up trials.

(6) ***Lift control (LC).*** LC trials were introduced to prevent competitors from assuming, over time, that the positions of the main-board cups were always switched when their line of sight was blocked after baiting (which would have enabled them to predict the

position of the baited cup in MI trials). LC trials were identical to MI trials with the sole exception that the main-board cups were lifted and placed back to their original positions instead of being switched.

Competitors always chose first while the participants' line of sight was blocked, participants always chose second. Competitors received a cup predetermined according to the theoretical prediction of an ideal choice (see above). In the UI and PI conditions, the predetermined choice was counterbalanced such that the remaining cup on the main-board contained the reward as often as it was empty. In the MI condition, the remaining cup always contained the reward whereas it was always empty in the FI condition. The agreement between the actual choice of the chimpanzee competitor and the predetermined choice was at chance levels for UI (44%, Cohen's $\kappa = -.10$, $N = 171$, $p = .161$) and low for PI (58%, $\kappa = .16$, $N = 181$, $p = .025$). Agreement for MI was 88% ($\kappa = .79$, $N = 183$, $p < .001$) and 88% for FI ($\kappa = .76$, $N = 183$, $p < .001$).

Sessions consisted of four trials per experimental condition and two trials per control condition (i.e., 20 trials per session in total). All trials within a session were of the same information type (i.e., all were 'knowledge' type trials or all were 'ignorance' type trials). OC trials occurred always as trial number 1 and 11, LC trials as trial number 6 and 16. Otherwise trials were pseudo-randomized such that no condition occurred more than twice in a row and such that the remaining main-board cup neither contained the reward nor was empty more than twice in a row.

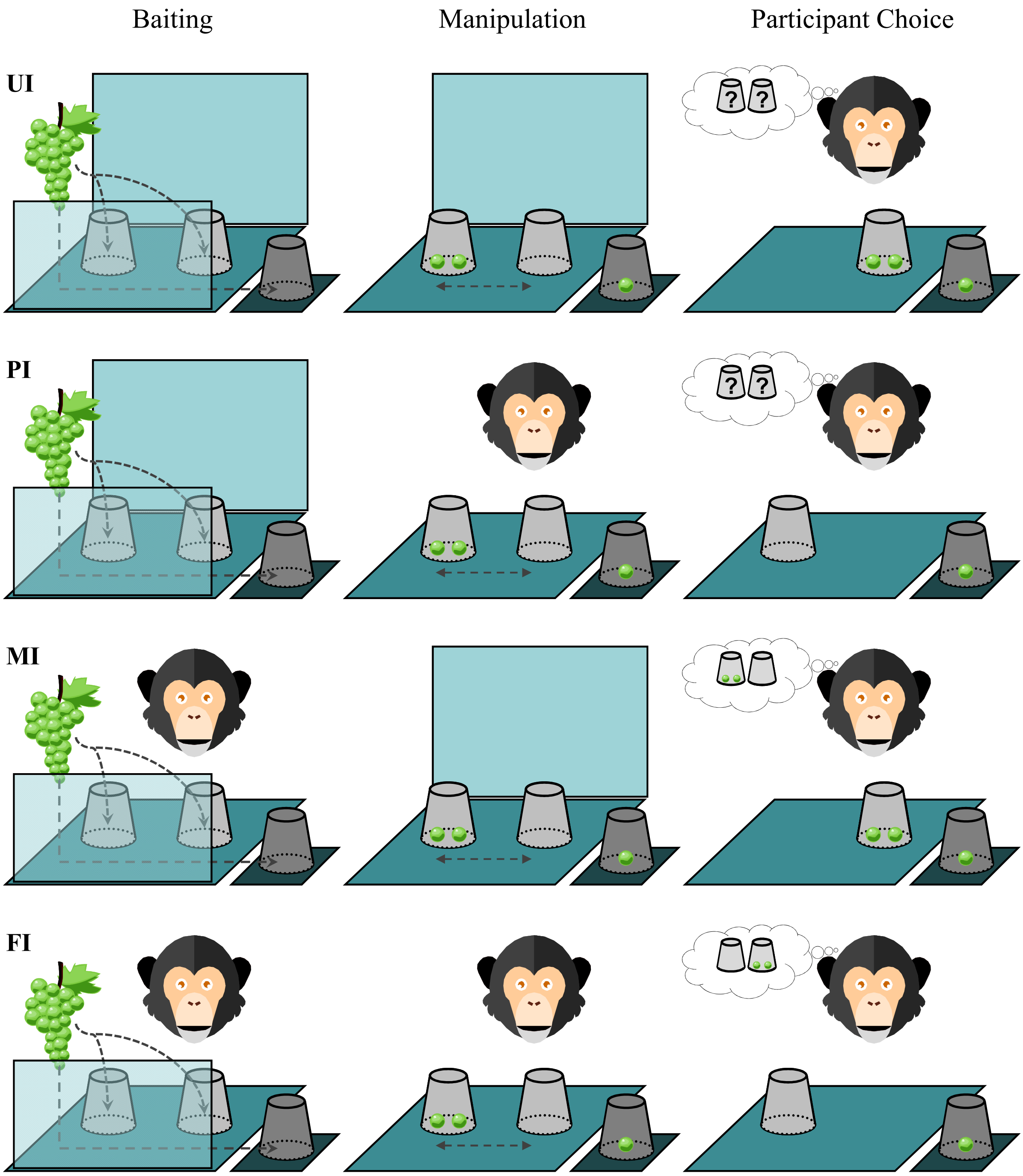

Figure 13. Test situation for ‘ignorance’ type trials from participants’ perspective before the initial baiting of the two cups (‘Baiting’), and the switching of the cups (‘Manipulation’), and after competitor has made a choice (‘Participant Choice’) for all experimental conditions (UI: uninformed, PI: partially informed; MI: misinformed, FI: fully informed); face visible: competitor observes event; face invisible: competitor’s line of sight is blocked; thought bubble: information that the competitor based his choice on; two light grey cups: main-board; dark grey cup: opt-out

Chimpanzees received two ‘knowledge’ type and two ‘ignorance’ type sessions on four consecutive days. Half of the chimpanzee participants started with a knowledge type session, followed by two ignorance sessions and another knowledge type session on the final day. For the other half of participants the order of the session types was reversed.

Children received one session of each type on two consecutive days. Half of the children received the ‘knowledge’ type session first, the other half received the ‘ignorance’ type session first.

Analysis. Trials were live coded and recorded by digital camcorders from different angles. Final scoring was confirmed via the video files. I scored whether participants chose the main-board cup or the opt-out cup. A second observer scored 22% of the trials to assess the inter-observer reliability of the participant choices. Agreement between coders was perfect (Cohen’s $\kappa = 1$).

Wilcoxon signed-ranks tests were used to compare the proportion of main-board cup choice in each condition against OC performance and to compare the proportion of main-board cup choice across information types within conditions. Further, a Generalized Linear Mixed Model (GLMM) analysis was conducted to assess the effects of the two predictor variables condition and information type on the ratio of main-board cup choice. Full models included the two main variables condition and information type, their interaction, as well as sex, trial order and participant random effects as fixed factors. All analyses were conducted using the statistic software R (R Core Team, 2014). Cup choice was modeled as binomial distribution via the lme4-package (D. Bates et al., 2015).

4.3.2 Results

The proportion of main-board cups that chimpanzees chose did not differ across information types in any of the conditions (Wilcoxon signed-ranks test; UI: $T_+ = 12.5$, $N = 5$, $p = .313$; PI: $T_+ = 8.5$, $N = 4$, $p = .375$; MI: $T_+ = 12.0$, $N = 6$, $p = 1$; FI: $T_+ = 8.5$, $N = 5$, $p = .938$; OC: $T_+ = 26.0$, $N = 8$, $p = .281$; LC: $T_+ = 15.0$, $N = 6$, $p = .531$; see Fig. 14). In all conditions, chimpanzees chose the main-board cup more often than in OC trials (UI: $T_+ = 78.0$, $N = 12$, $p < .001$; all others: $T_+ = 66.0$, $N = 11$, $p < .001$). Further, a GLMM revealed no significant overall effect of the variables information type and experimental condition on the proportion of main-board cup choice ($\chi^2 = 8.35$, $df = 7$, $p = .303$).

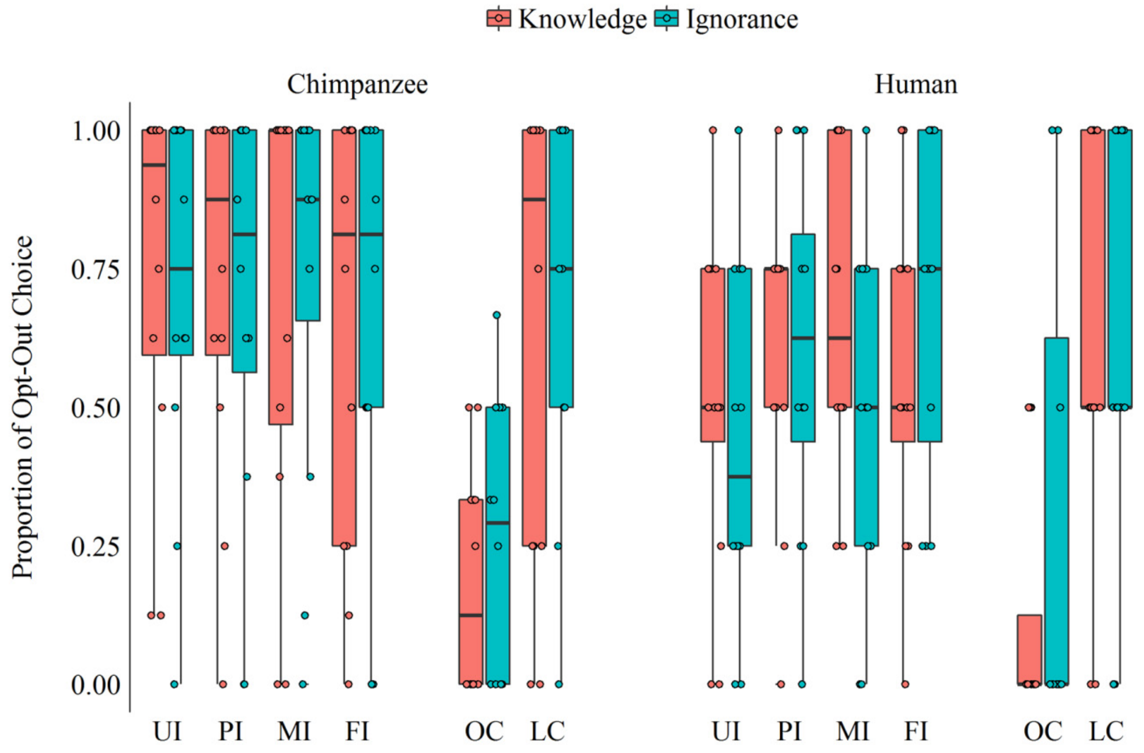

Figure 14. Average proportion of main-board cup choice for chimpanzees (left) and human children (right) across information types (red: knowledge, blue: ignorance), and conditions (UI: uninformed, PI: partially informed, MI: misinformed, FI: fully informed, OC: opt-out control, LC: lift control); box length: interquartile range; whisker length: 1.5 x interquartile length.

Like Chimpanzees, children's proportion of main-board cup choice did not differ across information types in any of the conditions (Wilcoxon signed-ranks test; UI: $T_+ = 40.0$, $N = 11$, $p = .600$; PI: $T_+ = 27.5$, $N = 10$, $p = 1$; MI: $T_+ = 39.5$, $N = 10$, $p = .250$; FI: $T_+ = 29.0$, $N = 8$, $p = .172$; OC: $T_+ = 12.5$, $N = 5$, $p = .313$; LC: $T_+ = 14.0$, $N = 7$, $p = 1$). In all conditions, children chose the main-board cup more often than in OC trials (UI: $T_+ = 61.0$, $N = 11$, $p = .009$; PI: $T+ = 75.0$, $N = 11$, $p = .002$; MI: $T_+ = 76.0$, $N = 12$, $p = .001$; FI: $T_+ = 78.0$, $N = 12$, $p < .001$; LC: $T_+ = 71.0$, $N = 14$, $p = .008$). A GLMM revealed no significant overall effect of the variables on the proportion of main-board cup choice ($\chi^2 = 8.33$, $df = 8$, $p = .402$).

4.3.3 Discussion

The chimpanzees' and children's choice of the main-board cup fitted neither the expectations of a performance based on the competitor's perceptual access nor the predictions of a performance exploiting the competitor's belief. Instead, chimpanzees and children showed no significant differences in their choices across conditions or information types. Again, this result is very surprising as many studies have established that chimpanzees do discriminate between knowledgeable and ignorant competitors and can modify their behaviour accordingly (e.g., Hare et al., 2001; Kaminski et al., 2008). For instance, the MI and the FI conditions were virtually identical to the 'unknown shift' and 'known shift' conditions respectively in the false belief study of Kaminski et al. (2008). The only differences were that (1) the main-board cup in the current experiment was contained a *higher amount* of reward instead of a *more preferred reward type* (which should rather lead to differences in motivation than in cognition), (2) two, instead of three, cups were used in the current experiment (which should have simplified the current task), and (3) when participants made their choice, there was only one cup remaining in the middle of the main-board in the current experiment, instead of all the cups at their initial positions in the study of Kaminski et al. (2008). Since both main-board cups were identical in appearance, their location was the only criterion by which they could have been discriminated. Thus, moving the remaining cup into the middle of the main-board might have had a similar effect as blocking participants' line of sight during the baiting, by disrupting participants' ability to implicitly assign the agent's knowledge and belief states to the respective cups (e.g., where would one expect participants to direct anticipatory looks in such a situation). Therefore, participants had to rely on their ability to explicitly reason about the competitor's belief. As Carruthers (2013) pointed out, it might be more demanding to acknowledge that an agent has some false belief without knowing what the belief is than being required to ascribe a specific belief to the agent which happens to be false. This could also be an explanation for the children's failure in the present task. Especially, as explicit belief reasoning is still subject to improvement at 5.5 year (Dumontheil, Apperly, & Blakemore, 2010).

4.4 General Discussion

I devised two non-verbal false belief tasks for chimpanzees with the goal of reducing inhibitory task demands and thereby revealing a potentially precluded explicit understanding of others (false) beliefs. The chimpanzees, as well as the control group of 5.5 year old preschool children, failed in both tasks albeit they were known previously to succeed in very similar paradigms (e.g., Kaminski et al., 2008; Karg et al., 2016; Schmelz et al., 2011, 2013); indicating that contrary to my goal the two tasks that I devised were more demanding.

Although I cannot exclude that my data failed to reach significance due to the small sample size, I do not think that this is a valid explanation of the results. First, for some conditions (including control conditions which encompassed a lower number of trials than in the experimental conditions) significance levels were reached. This deems it unlikely that the lack of statistical power per se was a problem. Second, other false belief studies with a comparable number of participants did not fail to find significant results (e.g., Call & Tomasello, 1999; Kaminski et al., 2008; Karg et al., 2016). Therefore, I rather think that the participants' failure is genuinely indicative of an increased task difficulty.

Chimpanzees in the same basic paradigm as the current studies have been shown to invert their own preference (e.g., for an iconic picture of food pieces unrelated to the contents of the respective container) if their competitor chooses first (Karg et al., 2016; Schmelz et al., 2013). Thus, having no preference, either due to both alternative choices being equally attractive, or remaining uninformed about the location of the preferred choice might have impeded chimpanzees' performance. However, this does not explain the children's failure or the chimpanzees' failure to exploit cues of the competitor's perceptual access. I therefore deem this explanation unlikely.

For the no preference task, the reason for the participants' failure might have been that the overall cognitive load was simply too high. Humans are thought to compare quantities via two distinct systems: an analog magnitude mechanism and an object file system (Feigenson, Dehaene, & Spelke, 2004). The latter is preferentially activated when comparing small quantities with set-sizes of up to four items and seems to require more cognitive recourses; as indicated by a study demonstrating that individuals switch to the analog magnitude system with higher cognitive load of the task (Hyde & Wood, 2011). Further, there is evidence that human adults' number judgments are impeded by the presence of another agent with a differing perspective (Qureshi et al., 2010). Although great apes seem to rely exclusively on the analog magnitude system when making quantity judgments (Cacchione, Hrubesch, & Call, 2014; Hanus & Call, 2007), they clearly possess the capacity to individuate and track objects through time and space (e.g., Mendes, Rakoczy, & Call, 2008). Some authors have speculated that the absence of a performance breakdown beyond the set-size limit of four (which is indicative of the object file system) might rather reflect an experimental confound of comparing human children to (mostly) adult apes than a true cognitive difference between species (Cacchione et al., 2014).

If the participants' failure in experiment 1 is due to a cognitive overload, this might be indicative of the chimpanzees and children in the current study individually representing (and memorizing) each reward piece. Thus it might be possible to reduce the cognitive load of the current task either by (1) allowing participants to see the contents of the cups up to when the competitor makes a choice (e.g., by using cups with a window allowing participants, but not competitors, to see the cups' contents; larger cups, completely blocking sight, could be put on these windowed cups just before competitors make their choice), (2) increasing the number of reward pieces under the HQ cup to more than four pieces and thereby promoting the use of the cognitively less demanding analog magnitude system of quantity judgment, or (3) employing two reward pieces differing in size, in place of different quantities of reward pieces.

The no knowledge paradigm of experiment 2 might have been too difficult as the task was taxing participants' capacity to explicitly reason about the competitor's belief while simultaneously denying all cues that could have helped to determine what this belief might have been. For instance, while the children in Call and Tomasello (1999) and Krachun et al. (2009) did not know the whereabouts of the reward they could at least see the target of the agent's belief (as the agent placed a marker on top of one of the containers or was reaching for one of them). If this was the reason for participants' failure in the current task, this would be in align with other studies which suggest that explicit and implicit belief understanding are interdependent (e.g., Low, 2010; Thoermer, Sodian, Vuori, Perst, & Kristen, 2012). More specifically, this would indicate that preschoolers' developing explicit belief reasoning is still dependent on cues triggering the implicit system—at least in a context that is not verbally eliciting an explicit response. However, standing in harsh contrast to this, others have found that in an object identity false belief task 4-year-olds and adults exhibit gazing towards the wrong target container but nevertheless give correct verbal answers (Low & Watts, 2013). Data from older children or human adults could also provide further insight into preschooler's failure in the current task.

In summary, my goal to devise two false belief tasks with reduced requirements for inhibitory control resulted in both tasks being more demanding than similar ones. Presumably, this was due to (1) a general cognitive overload caused by the necessity to keep multiple object representations in memory and (2) being required to rely on processes of explicit belief reasoning without the supporting role of any implicit belief detection processes highlighting the specific belief content. Overall, more studies further reducing cognitive load are required to elucidate the exact reasons for participants' failures in the two novel tasks of the present study.

5. General Discussion

5.1 Main Findings

The aim of the studies presented in the current thesis was to advance the insight into great apes understanding of others' visual perceptions and perceptual beliefs and thus also to further knowledge of how the human capacities of perspective-taking and ToM evolved within the hominid lineage.

In study 1 (Chapter 2), I investigated whether orangutans competing with a human experimenter for food would engage in perspective-taking to conceal their reaching for the food from the experimenter's line of vision. Whereas the orangutans were adept at exploiting the experimenter's body orientation as a cue to avoid his visual attention, they showed only a marginal preference to reach through an opaque tunnel (instead of a transparent one) in a situation where they could not observe orientational cues (as the experimenter was facing both tunnels). Further, they frequently only did so after initially inspecting the transparent tunnel and then switching to the opaque one. Considering only their initial inspections, the orangutans chose randomly between the opaque and the transparent tunnel, indicating that their final reaching was presumably driven by an egocentric behavioural rule than human-like perspective-taking. The results suggest that orangutans have a more limited understanding of other's perspectives than chimpanzees, who successfully chose the opaque tunnel directly from their starting position in the original study of Melis et al. (2006). Overall, orangutans seem to rely mainly on cues from facial and bodily orientation and egocentric rules when judging others' perspectives.

Study 2 (Chapter 3) explored great apes' and 20 month old human infants' communicative behaviour in a triadic request situation. More specifically, I investigated whether, and how, great apes and infants would direct a human experimenter's visual attention towards an object that was spatially and visually separated from the experimenter.

Infants and apes both adapted their signals to the attentional state of the experimenter, as well as to the location of the reward. Yet, while infants frequently positioned themselves in front of the experimenter and pointed towards the distant reward, apes either remained in the experimenter's line of sight predominantly pointing towards him, or moved out-of-sight pointing towards the reward. Further, when pointing towards a reward that was at a separate location from the experimenter, only the infants, and not the apes, took the experimenter's attentional state into account. These results demonstrate that prelinguistic human infants and nonhuman apes use different means when guiding others' attention to a location, indicating that differing cognitive mechanisms may underlie their pointing gestures.

In study 3 (Chapter 4), I examined chimpanzees' and 5.5 year old human children's understanding of perceptual beliefs. As chimpanzees, in studies to date, might have failed in explicit false belief tasks due to a lack of inhibitory control, I tried to design two novel competitive false belief tasks which did not require participants to inhibit a prepotent response. In the critical experimental condition of experiment 1 ('no preference task'), participants observed a series of hiding and manipulation involving two accessible containers. The containers held an equal amount of reward but the competitor falsely believed one of them held a higher amount. In the false belief situation of experiment 2 ('no knowledge task'), participants did not know where the reward was located but observed that the location of the two containers (one of which held the reward) were reversed, while the competitor's line of sight was blocked by a visual barrier. Chimpanzees' and children's performance did not fit the expectations of a strategy based on the competitor's perceptual access, or a strategy based on the competitor's belief. The results indicate that the two novel tasks were cognitively more demanding than other false belief tasks due to an increase in cognitive load (experiment 1) and the necessity to explicitly reason about the competitor's beliefs in absence of knowledge of specific belief contents (experiment 2).

5.2 Recent Theories of ToM Development in Humans

The finding that human infants exhibit sensitivity to others' belief-like states long before they are able to pass explicit verbal tests of false belief understanding (Baillargeon et al., 2010) has led to lively debates about the ontogenetic development of the human capacity of ToM. In the following, I will introduce two recent accounts of ToM development in children that both address the discrepancy between infants' early sensitivity to belief-like states and their failure in verbal explicit tasks of false belief understanding. Subsequently, I will try to relate these accounts to findings from comparative research with great apes and the results of the three studies presented here.

The nativist account (e.g., Baillargeon, Scott, & Bian, 2016; Baillargeon et al., 2010) construes a picture of infants' early sensitivity to the belief-like states of others' that is cognitively rich. Proponents of this account interpret infants' surprised reactions in looking-paradigms involving false belief situations as the first manifestation of an (presumably innate) unitary capability to perceive others' behaviour in terms of underlying mental states. This early developing module for psychological reasoning is supposed to operate without conscious awareness and assumed to be universal across cultures (e.g., Barrett et al., 2013) and thus supposedly constitutes an evolutionary ancient trait. It allows infants to understand others' motivational states, whether others are knowledgeable or ignorant about objects and events, and that others can have false perceptions (Song & Baillargeon, 2008) as well as false beliefs (e.g., Onishi & Baillargeon, 2005; Surian et al., 2007; Träuble, Marinović, & Pauen, 2010). According to the nativist account the early understanding of others' beliefs is wide-ranging and includes the understanding of false beliefs about object identities. The main evidence for the latter comes from a study conducted by Scott and Baillargeon (2009). In this violation-of-expectation paradigm, infants were habituated to a scene in which an agent repeatedly reached for a two-piece toy penguin that was split up in its two halves, while ignoring at the same time a one-piece toy penguin. Following each reaching, the agent placed a key in the bottom half of the two-piece penguin and reassembled both pieces such that it was finally indistinguishable from the one-piece penguin. In the false belief situation, the experimenter reassembled the two-piece penguin in absence of the agent and placed it beneath a transparent cover, whereas the one-piece penguin was placed beneath an opaque cover. The infants in the study reacted more surprised (as indicated by longer looking times) if the agent returning with the key reached for the transparent cover, than when she reached for the opaque cover (while showing the reversed pattern of surprise if the agent was present throughout the experimenter's initial manipulations). The authors interpret this result as indicating that the infants in their study expected the agent to mistake the assembled two-piece penguin for the one-piece penguin and thus to search for the two-piece penguin (that was always present in prior scenes) under the opaque cover.

Further, according to the nativist account, the early developing psychological reasoning systems also entails an understanding of others' as driven by the principle of rationality, that is, that agents will act in accordance to their mental states and pursue their goal with minimal effort (Baillargeon et al., 2010). Evidence for the latter comes from preferential looking studies in which infants have been habituated to the sight of an agent pursuing a goal with an indirect approach due to physical constraints (e.g., Gergely, Nádasdy, Csibra, & Bíró, 1995; Scott & Baillargeon, 2013; Sodian, Schoeppner, & Metz, 2004). When the constraints are removed, infants react more surprised if the agent continues to execute the original motion patterns of the indirect approach than when changing to the differing motion patterns of a more efficient direct approach. Moreover, 14-month-olds have been found to imitate rationally, that is, they are less likely to copy the details of an unusual (and less efficient) action if it appears to stem from physical constraints (Gergely et al., 2002).

In summary, according to advocates of the nativist account, infants' sensitivity to the false beliefs of others already indicates a fully blown understanding of beliefs (that might become more refined through the influence of language and executive function). Three-year-olds failure in explicit verbal false belief tasks is thought to be due to extraneous task demands, most prominently linguistic capabilities, and the necessity to inhibit the prepotent own knowledge of the true state of affairs when giving an answer.

The two-systems account (Apperly & Butterfill, 2009; Butterfill & Apperly, 2013; Low, Apperly, Butterfill, & Rakoczy, 2016) also assumes that infants possess an early developing system to track simple mental states, but postulates that humans acquire an additional second, later developing and more flexible system that is responsible for (effortful) explicit processes of reasoning about the mental states of others. The early developing (and evolutionary ancient) system 1 is supposed to be fast and efficient at the trade-off of being inflexible. According to this account, system 1 automatically tracks whether and where others have last registered (i.e., seen) an object but fails in situations that require explicit processes of reasoning about the mental states of others. The understanding of how others perceive an object (i.e., level-2 perspective-taking) or the understanding of beliefs about object identities are two mind reading skills that are beyond the limits of system 1. Around the age of 4 years—under the influence of language and a maturing executive function—children additionally acquire the second system for explicit reasoning about mental states that is cognitively more resource demanding than the first one. Thus, contrary to the nativist account, 3-year-olds failure in explicit false belief tasks is thought to be due to a conceptual lack (as system 2 is not developed yet).

Several studies have confirmed the specific signature limits predicted by the two-systems account. First, studies have shown that in tasks, in which participants have to judge the number of visual stimuli, responses are affected by altercentric interference (Kovács et al., 2010; Samson, Apperly, Braithwaite, Andrews, & Bodley Scott, 2010; Surtees, Samson, & Apperly, 2016), that is, participants show higher latencies in giving responses and increased error rates if an observer is present who has a differing perspective (i.e., is oriented such that only a subset of stimuli is visible from the observer's perspective). These results are thought to indicate the existence of a system that automatically (i.e., in absence of any explicit task demands) computes the perspective of other agents (in the sense of what the agent can and cannot see). In contrast, responses are not affected by unintentional altercentric interference in tasks requiring participants to judge how visual stimuli are perceived (Surtees, Butterfill, & Apperly, 2012; Surtees, Samson, et al., 2016). The authors interpret this as evidence for the limits of system 1 and as indication that level-2 perspective-taking is effortful and consciously initiated by processes of explicit reasoning.

A second signature limit predicted by the two-systems account originates from system 1 being limited to (automatically) tracking where others last registered an object, while at the same time being incapable of computing others' beliefs about object identities. To demonstrate this signature limit, Low and Watts (2013) modified the classic unobserved change-of-location false belief paradigm into an unobserved change-of-identity false belief paradigm (see also Low, Drummond, Walmsley, & Wang, 2014; Wang, Hadi, & Low, 2015). In the familiarization phase of this task, participants observed a blue object moving from one container to the other, and subsequently a red object moving from the second container to the first one (where the blue object started its movement). An agent observing these events would always reach for the blue (or red) object indicating a clear preference to attain objects from the one (but not the other) colour. In the test phase of the task, there was only one object present (a toy robot), however with one side being coloured blue and the other one being coloured red. In the false belief condition, the agent observed the robot moving from the first container to the second with the blue side facing the agent. In the second container—observed by the participant but not by the agent—the robot rotated such that its blue side was now facing away from the agent. Then the robot moved back to the starting container (this time with the red side facing the agent), leading the agent to the false belief that the blue robot still remained in the second container. While 4-year-olds and adults gazing indicated that they expected the agent to search in the second container (where the robot rotated to reveal its other side), they nevertheless gave correct verbal answers when explicitly asked in which container the agent would search (cf. F. Buttelmann et al., 2015; Scott & Baillargeon, 2009). Proponents of the two-systems account see the results as confirmation of the predicted signature limit of system 1. Further, they interpret the discrepancy of participants' gazing behaviour and their explicit verbal answers as evidence for the persistence of two largely independent systems into adulthood.

5.3 Ape Comparative Research and Human ToM Development

Great apes, like human infants, seem to understand (some of) the behaviours of others in terms of their underlying mental states. As already mentioned in Chapter 1 of this thesis, evidence from various studies indicates that all great apes can recognize goals and intentions and seem to be able to discriminate some emotions as happiness and disgust. Further, great apes appear to have a good understanding of visual attention and of what others can and cannot see in the present as well as of what they have and have not seen in the past (i.e., whether others are knowledgeable or ignorant). However, as the results of study 1 demonstrate, great apes apparently differ in their level-1 perspective-taking skills. Orangutans' understanding of others' perspectives seems to be focused on facial and bodily orientation whereas chimpanzees are additionally capable of more human like (level-1) perspective-taking (see Melis et al., 2006). Theoretically, this difference might be due to competitive tasks being better suited to elicit more socio-cognitive skills in chimpanzees than in orangutans, as the former also face a higher degree of intraspecific competition in the wild.

However, results from tasks in cooperative communicative contexts also support the view that orangutans' perspective-taking is less sophisticated (Liebal, Pika, Call, et al., 2004; Okamoto-Barth et al., 2007). Taken together the data suggests an evolutionary progression from more simple forms of perspective-taking in orangutans to more sophisticated perspective-taking skills in chimpanzees and humans. Yet, due to their solitary lifestyle orangutans might also have lost perspective-taking skills that were already present in a common ancestor of the great ape clade, as already discussed in Chapter 2. In this regard, it is noteworthy that Forss, Willems, Call, and van Schaik (2016) have found cognitive differences between Bornean (*P. pygmaeus*) and Sumatran (*P. abelii*) orangutans, whose lineages split up only about 0.9–1.1 Ma ago (Mattle-Greminger, 2015). In several standardized non-verbal tasks devised to test participants' physical cognition and inhibitory control, they found zoo-living Sumatran orangutans to perform better than their zoo-living Bornean counterparts. The authors assume that higher population densities and increased social tolerance in Sumatran orangutan population have provided more opportunities for social learning and thus led in turn to evolutionary differences in cognitive skills between these two species. Although the test battery of Forss et al. (2016) did not include tasks to directly investigate socio-cognitive skills, it is easy to imagine that such tasks would have yielded comparable differences. Therefore, drawing firm conclusions about the evolutionary trajectory of perspective-taking skills in the great ape clade seems premature before more detailed data about gorilla and bonobo perspective-taking is available.

Nevertheless—at least judging from what is known about chimpanzee mind reading skills—the data overall supports the assumption of an evolutionary ancient ToM module shared by humans and the other great apes. Chimpanzees show comparable skills and limitations in regards to reading others' minds as young infants do below the age of 4 years. For instance, while a recent study demonstrated an implicit sensitivity to belief-like states (Krupenye et al., 2016), no study to date could provide evidence for an explicit understanding of others beliefs (Call & Tomasello, 1999; Kaminski et al., 2008; Krachun et al., 2009, 2010; O'Connell & Dunbar, 2003). As discussed earlier (see Chapter 4), this might be due to chimpanzees' sensitivity to belief-like states being masked by their lack of inhibitory control. Also study 3 in which I attempted to devise two false belief paradigms with reduced demands for inhibitory control did not reveal any belief understanding in chimpanzees. However, as the control group of 5.5 year old children—who are known to be capable to succeed in explicit verbal tests of false belief understanding—also failed in those tasks, unfortunately, no new insights are gleaned from the chimpanzees' failure in study 3.

Besides an explicit understanding of false beliefs, chimpanzees seem to also lack the capability to engage in level-2 visual perspective-taking. Studies indicate that they rather rely on self-experience and self-preference to infer how others' visually perceive objects, and that they fail to make these judgements in situations in which they lack these attributes (Karg et al., 2016). While self-experience and self-preference also play a role in human perspective judgements (e.g., Meltzoff & Brooks, 2008), human children from an age of 3–4 years can also engage in level-2 perspective-taking without the immediate help of both (e.g., Karg et al., 2016; Moll & Meltzoff, 2011b; Pillow & Flavell, 1986).

Great apes' failure in tasks that require an explicit false belief understanding and level-2 perspective-taking seems to be more in line with the two-systems account of human ToM development (Apperly & Butterfill, 2009; Butterfill & Apperly, 2013; Low et al., 2016), which attributes these skills to the late developing and flexible system of explicit reasoning about the mental states in others. Theoretically, both capabilities could be masked by a lack of inhibitory control, as suggested by the nativist account for human infants below the age of around 4 years of age; however, Karg et al. (2016) demonstrates that, at least for level-2 perspective-taking, this appears to be unlikely. Reducing self-preference for one of the alternative choices, thereby in turn increasing demands for inhibitory control, led to a breakdown of the participants' success in the task instead of improving their performance.

5.4 Joint Attention and ToM

Moll and Meltzoff (2011b, 2012) point out the importance of joint attention in the development of an understanding of others differing beliefs and perspectives. Through the experience of sharing attention on objects or events infants gradually learn that one and the same entity can be viewed, construed and conceptualized in various ways depending on the other's point of view (Perner, 2000; Perner, Stummer, Sprung, & Doherty, 2002). Language and other communicative behaviours, such as pointing, might facilitate this process by directing attention towards and differentially highlighting various aspects and perspectives on the joint focal object (Moll & Meltzoff, 2012). Also studies with human adults who already possess a fully developed ToM point towards a special role of establishing joint attention and joint goals in taking the perspectives of others'.

In the mental rotation paradigm of Böckler, Knoblich, and Sebanz (2011), two human adults sat opposite each other and were attending to two subsequent pictures of hands placed in-between both participants. The participants' task was to judge whether or not the second picture that was rotated by various degrees corresponded to the handedness of the first one. While participants' error rates and reaction times increased the more the second hand was rotated towards the other participant, this effect was less pronounced when their partners were jointly attending; with their eyes open as opposed to closed (i.e., participants engaged in joint attention performed worse in easy trials with a low angular displacement and performed better in difficult trials with a high angular displacement). This indicates that participants jointly attending a stimulus with others adopted more of an allocentric reference frame instead of an egocentric one (see also Böckler & Zwickel, 2013; Tversky & Hard, 2009).

Similar results were found by Freundlieb, Kovács, and Sebanz (2016). In a stimulus response task, two human adults sitting at a 90° angle to each other and jointly attended to the same array of stimuli, where participants' response buttons were arranged such that they reflected the confederates' (horizontal) perspective onto the array (whereas the participants' perspective onto the array was vertical). If the confederate was actively engaged in the task, participants' responses were faster than when the confederate was just passively observing, indicating that the joint engagement elicited a spontaneous adoption of the confederate's visuospatial perspective.

In a task of Surtees, Apperly, and Samson (2016), participants and confederates were sitting opposite to each other and had to judge whether the magnitude of a digit that was presented on a screen, in-between the participants, was above or below seven. Whereas some of the digits (5 and 8) looked the same from the participant's and the confederate's perspective, others (6 and 9) appeared up-side down from the confederate's side (implying inconsistent magnitude judgements). While being equally efficient at judging consistent and inconsistent digits when completing the task alone, participants being conjointly engaged in the task with a confederate made more errors and responded slower when making magnitude judgements about inconsistent digits.

Whereas joint attention appears to be particularly important for humans, it seems to be considerably less fundamental in great apes. Although standard reared captive great apes are known to follow the gaze of others to out-of-sight targets, and have been reported to alternate their gaze between a target and communicative partners (Leavens & Hopkins, 1998; Leavens, Hopkins, & Bard, 1996; Leavens, Hopkins, et al., 2004), some scientists assert that this co-attendance is qualitatively different from episodes of joint attention in humans (Carpenter & Call, 2013). Carpenter and Call (2013) argue that in contrast to human joint attention episodes of co-attendance in great apes lack the mutual intention to share sights with each other and thus they constitute a form of parallel attention to the same object. Supporting this claim, standard captive-reared great apes fail to recognize the communicative intent of pointing, as indicated by an external referent. This holds true for cooperative (Herrmann, Melis, & Tomasello, 2006) as well as competitive (Tempelmann et al., 2013) contexts. Further, great apes employ their gestures for imperative but not for declarative purposes (e.g., Bullinger et al., 2011). In line with this, the performance of the great apes in study 2 of the current thesis supports a lean account of great ape pointing. They demonstrated sensitiveness to the experimenter's attentional state, as well as the reward location, by adjusting their visual gestures accordingly, but failed at the same time to employ their pointing triadically to inform the experimenter about the reward. In the critical experimental condition, they either remained in front of the experimenter and pointed towards him or moved out of his line of sight to point to the reward. Their pointing to the other side was influenced by the reward location but not by the experimenter's attentional state. Contrary to that, 20 month old infants instead positioned themselves in the experimenter's line of sight, pointing from there towards the reward. Their pointing to the other side was affected by the reward location as well as the experimenter's attentional state.

While their pointing allows humans to direct attention to distal targets, great apes seem to be mostly limited to moving into close proximity of the intended referent (see van der Goot et al., 2014 for similar results) which would presumably drastically reduce available opportunities to share attention with others. If Moll and Meltzoff (2012) are correct with their assumption that joint attention is crucial in the development of an explicit ToM (which seems to correspond to the supposed late developing and flexible system 2 in the two-systems account) the lack of (or the limited opportunities for) joint attention in great apes could also provide an explanation for great apes' failure to acknowledge others' beliefs and level-2 perspectives.

In summary, as of now it seems that great apes have an understanding of other minds comparable to young infants who still rely on the early developing and inflexible ToM system 1. A main difference, however, between great apes and young infants, remains the lack of (motivation to engage with others in episodes of) joint attention in great apes. This lack (in addition to the lack of linguistic input) might in turn prevent great apes from developing a flexible and explicit ToM as possessed by human children above the age of around 4 years.

5.5 Sample Considerations

As a final caveat to all that has been said above about supposed differences between species, I will discuss considerations regarding the sample compositions in the three studies presented here. All the great apes studied in my thesis were raised in captivity. Clearly rearing conditions and experience from social and environmental inputs during ontogenesis can have a marked impact on individuals' behaviour and cognition (e.g., Bogart, Bennett, Schapiro, Reamer, & Hopkins, 2014; Morimura & Mori, 2010; J. L. Russell, Lyn, Schaeffer, & Hopkins, 2011). Captive held great apes, even if raised by their mothers, do not encounter many of the challenges that their wild living counterparts face. For instance, they are neither exposed to predatory pressure nor are they forced to engage in hunting or any sophisticated foraging strategies, as they are supplied with food by humans (although most modern zoos try to compensate for the latter by providing various food enrichment techniques). While these impoverished conditions might have detrimental consequences for the captive animals' cognitive abilities, captivity and close human contact can also lead to a performance increase for behaviours not observed in the wild. For instance, while there are only a few reports of pointing in wild great apes (Douglas & Moscovice, 2015; Veà & Sabater-Pi, 1998), great apes in captivity frequently exhibit communicative pointing, sometimes without being trained to do so (Leavens & Hopkins, 1999). Presumably this is due to the physical constraints preventing captive great apes from gaining access to desirable food on their own. This in turn might promote the acquisition of pointing as a communicative behavioural means to socially manipulate human caretakers in order to receive these out of reach food items (Leavens, 2004). Pointing behaviour might be even more enhanced when the offspring is separated from their natural mothers and raised under human-like ‘enculturated’ conditions (Lyn et al., 2010; J. L. Russell et al., 2011). Thus, while it is clear that captivity and artificial rearing conditions can change cognitive capabilities, the direction of change does not seems to be straightforward and predictable. Therefore, generalizations from standard reared captive ape samples to the whole species should only be made with great caution (strictly speaking they are impossible without data from various rearing conditions converging in the same direction).

Because of practical limitations my great ape species samples were restricted to individuals from single captive held groups (with the exception of study 2 in which the chimpanzee sample was split up into two separate groups housed in neighbouring enclosures of the same facility). While making valid claims about the cognitive trait of a whole species based just on captive populations seems delicate enough, it is even more difficult to make these inferences just based on single captive groups. In all wild great apes, considerable behavioural variation has been observed within and between populations (bonobos: Hohmann & Fruth, 2003; orangutans: Krützen et al., 2011; gorillas: M. M. Robbins et al., 2016; chimpanzees: Whiten et al., 1999), sometimes even between closely neighboured groups living under very similar environmental conditions (Luncz, Mundry, & Boesch, 2012). Although all great apes in the studies presented here were held captive, their daily routines, their (in- and out-door) habitats and presumably the specifics of their interactions with the local keeper staff differed in some detail. This theoretically could have led to differences in behaviour (and underlying cognitive traits).

In juxtaposition, while most of what is known about human cognition stems from studies in western educated industrialized democratic ('WEIRD'; Henrich, Heine, & Norenzayan, 2010) countries, there is also great behavioural variation across various human cultures (e.g., Henrich et al., 2010). Considering the human capacity of ToM, cross cultural studies have found differences in the onset of an explicit verbal ToM (as indicated by success in classic verbal tests of false belief understanding). Whereas WEIRD children typically pass false belief tasks at the age of around 4 years (Wellman et al., 2001), children from some non-western countries show a delayed ToM development, sometimes with a majority not succeeding before 8 years of age (e.g., Callaghan et al., 2005; Knight, Sousa, Barrett, & Atran, 2004; Liu et al., 2008; Mayer & Träuble, 2013; Vinden, 1999). As of yet, the data is still unclear and in some cultures ToM developmental trajectories might be even more prolonged (e.g., De Gracia, Peterson, & de Rosnay, 2016). However, eventually all normally developing humans exhibit a false belief understanding at some point, even in cultures with an 'opacity of mind doctrine' (J. Robbins & Rumsey, 2008) in which mental state talk is more or less strongly discouraged (Callaghan et al., 2005; Mayer & Träuble, 2013; Oberle, 2009). Cross cultural data for an early developing implicit false belief understanding is still too patchy to draw firm conclusions, but first results suggest a higher consistency in developmental trajectories (Barrett et al., 2013). Thus, notwithstanding great variance across different cultures and parenting styles, at least in humans the ToM capacity seems to be a very robust phenomenon.

With all the above being said, I am nevertheless convinced that the data presented in my thesis constitutes a valuable contribution to the understanding of great apes' perspective-taking and mind reading skills. However, instead of seeing it as a definite answer to questions in the field, the results presented here (as well as others presented elsewhere) should rather be treated as starting points for further replications with other captive (and—so far as possible—wild) populations to gain a clearer picture of the respective great ape species in general. Only then will it be possible to draw firm conclusions about the evolutionary origins of the human ToM.

6. Summary

Premack and Woodruff (1978) were the first to coin the term 'Theory of Mind' denoting individuals who understand themselves and others as agents whose actions are driven by unobservable psychological states. While this understanding encompasses various aspects of others' minds (such as intentions, perceptions and beliefs), the most thoroughly studied domain is the understanding of others' visual perceptions. At the start of their second year of life, human infants already conceptualize the gazing of others' as 'seeing' and understand what objects others can and cannot see from their perspective (level-1 visual perspective-taking; Flavell, 1992). Around that time, they also start to direct the focus of others' visual attention to external entities (as objects and events) by gestural means, such as pointing. By sharing experience with others in bouts of joint attention (either established by following or directing others' visual attention), around the age of 4 years, they are thought to come to the understanding that the same object can appear differently from other perspectives (Moll & Meltzoff, 2012); that is, amongst others *how* others perceive objects (level-2 perspective-taking; Flavell, 1992). Paralleling this, children at the same age also start to grasp that others can hold (false) beliefs that differ from their own, as well as the 'true' state of affairs.

In my dissertation, I aimed to contribute to a more complete understanding of a ToM exploring its evolutionary roots. To this end, I investigated great apes' understanding of others' visual perceptions and perceptual beliefs. Like human infants, apes have been found to follow the gaze of others to out-of-sight targets and around visual barriers. Furthermore, they understand what others can and cannot see from their perspective, and that others need to be visually attentive in order to react to behaviour. They flexibly employ this knowledge in a variety of communicative and competitive situations (reviewed in Call & Tomasello, 2008). A novel study exploring 'implicit' behavioural measurements (such as gaze) has even revealed sensitivity to the (false) perceptual beliefs of others (Krupenye et al., 2016). In this study, the apes expected an agent to search at the location where he last saw the desired object (or individual), even when the actual location had changed in the meantime.

Although much has been discovered about ape mind reading skills in general and their understanding of others' visual perceptions in particular, scientific gaps still prevent us from gaining a more coherent picture of these traits. In my thesis, I attempted to partially bridge three of those gaps in the extant literature. For instance, most of what is known about apes' understanding of other perspectives, stems from studies with chimpanzees—especially when it comes to competitive situations. Therefore, one goal of my thesis was to extend the current state of knowledge about great ape mind reading by investigating orangutans' perspective-taking skills in a competitive food paradigm (study 1). Furthermore, although it is well established that all apes adapt their communication to the recipient's visual attention (e.g., by producing less visual gestures when the recipient is inattentive), it remains unclear whether they communicate to manipulate others' behaviour or others' mental states (e.g., by informing). Thus, another goal of my thesis was to address this question by investigating whether apes point to direct others' focus of visual attention (study 2). Finally, in response to the findings of Krupenye et al. (2016), which demonstrate that apes expect others to act according to their false beliefs (indicated by the direction of anticipatory looks), the third goal of my thesis was to examine whether this discrepancy to great apes' failure in tasks that required a more explicit understanding of false beliefs (e.g., indicated by their choice behavior), was due to extraneous task demands (study 3).

In study 1, I investigated orangutans' understanding of others' visual perspectives in a competitive setting. In the task, participants had to reach through one of two opposing plexiglass tunnels in order to retrieve a food reward. Both rewards were also physically accessible to a human competitor sitting opposite the participant. As soon as the competitor saw a participant reaching for the food, he would remove the respective piece. Participants always had the possibility of reaching one piece of food that was outside the human's line of sight. This was because either the human was oriented to one, but not the other reward, or because one tunnel was covered by an opaque barrier and the other remained transparent. In the situation in which the human was oriented towards one reward, the orangutans successfully avoided the tunnel that the competitor was facing. If one tunnel was covered, they reached marginally more often through the opaque versus the transparent tunnel. However, they did so frequently after initially inspecting the transparent tunnel (then switching to the opaque one). Considering only the participants' initial inspections, they chose randomly between the opaque and transparent tunnel, indicating that their final decision to reach for the reward was probably driven by a more egocentric behavioural rule. Overall, the results suggest that orangutans have a limited understanding of others' perspectives, relying mainly on cues from facial and bodily orientation and egocentric rules when making such judgements.

In study 2, I explored whether apes and 20 month old human infants would use communicative means to direct others' visual attention towards an external referent. To this end, I designed a task in which participants were requesting a desired reward from a human experimenter. I systematically varied the experimenter's visual attention (i.e., they were oriented toward or away from the participant) as well as the location of the reward (separated by a visual barrier from the experimenter or not). Apes and infants both adapted their signals to the attentional state of the experimenter, as well as to the location of the reward. However, while infants frequently positioned themselves in front of the experimenter and pointed towards a reward that was placed at a distance, apes either remained in the experimenter's line of sight pointing towards him, or moved out-of-sight pointing towards the reward. Further, when pointing towards a distant reward, only the infants and not the apes took the experimenter's attentional state into account. These results demonstrate that prelinguistic human infants and nonhuman apes use different means when guiding others' attention to a location, indicating that differing cognitive mechanisms may underlie their pointing gestures.

In study 3, I examined chimpanzees' and 5.5 year old human children's understanding of perceptual beliefs. As chimpanzees might have failed in previous explicit false belief tasks due to a lack of inhibitory control, I tried to design two novel competitive false belief tasks that did not require participants to inhibit a prepotent response. To this end, I modified the basic paradigm employed by Kaminski et al. (2008). In this paradigm, the participants took turns with a conspecific competitor choosing from opaque cups that contained hidden rewards. Each trial started with participants observing a series of manipulation of the cups. Depending on experimental conditions, competitors either saw all the manipulations, only a subset, or none at all. Finally, competitors chose one of the cups without the participants watching. Thus, participants had to base their own choice on what their competitor had or had not seen. In the critical experimental condition of the first task ('no preference task'), participants knew that both cups held an equal amount of reward whereas the competitor falsely believed one of the containers to hold a higher amount of reward. In the false belief situation of the second task ('no knowledge task'), participants did not know where the reward was located but observed that the location of the two containers (one of which held the reward) was reversed while the competitor's line of sight was blocked by a visual barrier. Chimpanzees' and children's performance fitted neither the expectations of a strategy based on the competitor's perceptual access, nor a strategy based on the competitor's belief. The results indicate that the two novel tasks were cognitively more demanding than other false belief tasks due to an increased demand on executive functioning (experiment 1) and the necessity to explicitly reason about the competitor's beliefs in absence of knowledge of specific belief contents (experiment 2).

Recent developmental and comparative ToM research indicates similar levels of competencies, as well as comparable limitations, in apes and children below the age of four. For instance, both are sensitive to others' false beliefs but fail at the same time to demonstrate more explicit forms of false belief understanding. Since my modified false belief tasks in study 3 turned out to be cognitively more demanding than similar tasks, it remains unclear whether this is due to extraneous demands or a conceptual lack. Although the data overall supports the assumption of an evolutionary ancient ToM module shared by humans and apes, my research also points out some relevant differences. Study 1 and other data indicates an evolutionary progression from more simple forms of perspective-taking in orangutans to more sophisticated perspective-taking skills in chimpanzees and humans. Study 2 reveals that great apes are less proficient at directing others' visual attention to distal referents than human infants. This difference in communicative strategies presumably leads to more limited opportunities for sharing experiences with others in bouts of joint attention. As mentioned above, some have suggested that repeatedly sharing differing perspectives on the same entity provides the experiental basis for understanding the subjectivity of perceptions (Moll & Meltzoff, 2012). Thus, the lack of communicative means to direct others' attention to external referents—might it be due to cognitive restraints or a lack of motivation—provides a potential explanation for apes' failure to acknowledge others' beliefs and level-2 perspectives.

In summary, the ape data seems to support the novel two-systems account of ToM development, postulating an evolutionary ancient, early developing fast and inflexible ToM module that is capable of automatically tracking some simple mental states (e.g., where others have last seen an object). Around the age of 4 years—under the influence of language and a maturing executive function (fueled by more pervasive joint attention experiences) —human children additionally acquire a second, more flexible system for explicit reasoning about mental states. This second system, that seems to be absent in apes, includes the conceptual understanding that one and the same entity can be construed in different ways, depending on subjective perspectives.

7. Zusammenfassung

Premack und Woodruff prägten in ihrer wegweisenden Arbeit aus dem Jahr 1978 als erste den Begriff ‘Theory of Mind’ („ToM“). Hiermit bezeichneten sie Individuen, die die eigenen Handlungen sowie die Anderer als durch äußerlich nicht beobachtbare psychologische Zustände motiviert begreifen. Obwohl sich diese Fähigkeit auf verschiedene Arten von Bewusstseinsvorgängen erstrecken kann (wie z.B. Gefühle, Absichten, Erwartungen und Überzeugungen), ist sie im Bereich der visuellen Wahrnehmungen Anderer am besten erforscht. Kleinkinder fassen bereits zu Beginn ihres zweiten Lebensjahrs die Blicke Anderer als Sinneswahrnehmung „Sehen“ auf und können beurteilen, welche Objekte jemand aus seinem Blickwinkel erkennen kann und welche nicht (sog. „Level-1 Perspektivübernahme"; Flavell, 1992). In diesem Alter fangen Kleinkinder auch an, den Fokus der visuellen Aufmerksamkeit Anderer mittels Gesten wie Zeigen gezielt auf Objekte und Ereignisse zu lenken. Dadurch, dass sie ihren Aufmerksamkeitsfokus mit Anderen teilen und dabei subjektive Eindrücke austauschen, erlernen Kinder im Alter von ungefähr 4 Jahren, dass ein und dasselbe Objekt aus unterschiedlichen Perspektiven unterschiedlich wahrgenommen werden kann (Moll & Meltzoff, 2012) und wie Andere Objekte wahrnehmen (sog. „Level-2 Perspektivübernahme"; Flavell, 1992). Im selben Alter beginnen Kinder auch zu verstehen, dass Andere von den eigenen und der Realität abweichende Fehlannahmen (sog. „false beliefs“) haben können.

Indem ich mich in der vorliegenden Dissertation mit den evolutionären Ursprüngen der ToM auseinandersetze, möchte ich zu einem besseren Verständnis dieser Fähigkeit beitragen. Hierzu untersuchte ich, was Menschenaffen (*Hominidae*) über die visuellen Wahrnehmungen und die sich daraus ableitenden Annahmen Anderer wissen. Von Menschenaffen ist bekannt, dass sie—wie Menschen im Kindesalter—Blicke um Hindernisse herum zu Zielen außerhalb ihres Sichtfeldes geometrisch nachverfolgen können. Außerdem erkennen sie, was Andere aus ihrem Blickwinkel heraus sehen können, und wissen, dass Andere visuell aufmerksam sein müssen, um auf Verhalten zu reagieren. Wie verschiedene Studien belegen, sind Menschenaffen dazu in der Lage, dieses Wissen flexibel in ihrer Kommunikation sowie verschiedenen Konkurrenzsituationen einzusetzen (s. Call & Tomasello, 2008). Durch eine Untersuchung sog. „impliziter“ Verhaltensweisen (wie Blicken) konnte in einer aktuellen Studie nachgewiesen werden, dass Menschenaffen auch für fremde Fehlannahmen empfänglich sind (Krupenye et al., 2016). So zeigten Menschenaffen in dieser Studie die Erwartung, dass Andere dort nach einem Objekt (oder Individuum) suchen werden, wo sie es letztmalig gesehen haben, selbst wenn es sich mittlerweile de facto an einem anderen Ort befindet.

Auch wenn Forscher in den vergangenen Jahren viel darüber herausfinden konnten, was Menschenaffen über die Gedanken und visuellen Wahrnehmungen Anderer wissen, existieren nach wie vor zahlreiche Wissenslücken. In meiner Dissertation habe ich den Versuch unternommen, drei dieser Lücken teilweise zu schließen und somit zu einem vollständigeren wissenschaftlichen Verständnis dieser Fähigkeiten beizutragen. So beruhen die meisten Erkenntnisse über die Fähigkeit der Menschenaffen zur Perspektivübernahme auf Verhaltensstudien an Schimpansen—dies gilt insbesondere für deren Verwendung in Konkurrenzsituationen. Daher war ein Ziel meiner Arbeit zu untersuchen, ob Orang-Utans die visuelle Perspektive eines menschlichen Experimentators einnehmen können, mit dem sie um Nahrung konkurrieren (Studie 1). Man weiß, dass Menschenaffen ihre Kommunikation an die visuelle Aufmerksamkeit des Rezipienten anpassen—z. B. indem sie weniger visuelle Gesten an unaufmerksame Rezipienten adressieren. Dennoch ist nach wie vor unklar, ob Menschenaffen beim Kommunizieren lediglich das Ziel verfolgen, fremdes Verhalten zu manipulieren, oder ob sie dabei auch auf die diesem zugrunde liegenden Gedanken Einfluss nehmen wollen (z. B. durch das Teilen von Informationen). In meiner Dissertation ging ich dieser Frage auf den Grund, indem ich untersuchte, ob Menschenaffen beim Zeigen die

Absicht verfolgen, die Aufmerksamkeit des Rezipienten auf den Referenten (d. h. das Ziel des Zeigens) zu lenken (Studie 2). In der bereits erwähnten Studie von Krupenye et al. (2016), erwarteten Menschenaffen, dass Andere Verhaltensweisen zeigen würden, die deren Fehlannahmen entsprechen. Dieser Befund ist insofern einzigartig, da Schimpansen bisher in allen Studien scheiterten, in denen ein „explizites“ Verständnis (z. B. gemessen am Wahlverhalten zw. mehreren Alternativen) solcher Fehlannahmen erforderlich war. Das dritte Ziel meiner Dissertation war es, zu untersuchen, ob diese Diskrepanz von Faktoren abhängt, die nicht direkt mit diesem Verständnis in Zusammenhang stehen.

In Studie 1 untersuchte ich die Fähigkeit von Orang-Utans zur visuellen Perspektivübernahme. Die Aufgabe der Probanden bestand dabei darin, sich eine von zwei Futterbelohnungen zu sichern, die sie durch zwei gegenüberliegende Tunnel aus transparentem Plexiglas ergreifen konnten. Ein menschlicher Gegenspieler, der den Probanden gegenüber saß, konnte ebenfalls beide Belohnungen erreichen. Sah dieser, wie ein Proband nach dem Futter griff, entfernte er das entsprechende Futterstück, bevor es der Proband zu fassen bekam. Die Probanden hatten allerdings stets die Möglichkeit, an eine der beiden Belohnungen zu gelangen, da sich diese außerhalb des Sichtfeldes des Gegenspielers befand. Je nach experimenteller Bedingung war dies entweder der Fall, weil (1) der Gegenspieler von dem einen Tunnel ab-, aber dem Zweiten zugewandt war, oder (2) weil der eine Tunnel durch eine Sichtblende verdeckt wurde, aber der Zweite unverdeckt blieb. Wenn der Gegenspieler zu einer der beiden Belohnungen orientiert war, mieden die Orang-Utans den entsprechenden Tunnel. War der Gegenspieler zu beiden Tunneln hin orientiert aber einer der beiden Tunnel verdeckt, griffen die Orang-Utans nur marginal häufiger durch den verdeckten Tunnel. Allerdings inspizierten viele unter ihnen zunächst den unverdeckten Tunnel und wechselten erst dann auf die gegenüberliegende Seite. Eine Analyse der Erstinspektionen ergab, dass sich Orang-Utans initial dem verdeckten bzw. unverdeckten Tunnel mit zufälliger Wahrscheinlichkeit näherten. Ihre finale Entscheidung beruhte also vermutlich eher auf egozentrischen Verhaltensregeln (wie z. B., „wechsle zum anderen Tunnel wenn der Gegenspieler sichtbar ist“) als auf Abwägungen der gegnerischen Perspektive. D. h., Orang-Utans scheinen nur über ein eingeschränktes Verständnis fremder Perspektiven zu verfügen und in erster Linie anhand von Körperausrichtung und egozentrischen Regeln einzuschätzen, was Andere sehen.

In Studie 2 untersuchte ich, ob und welche kommunikative Mittel Menschenaffen und 20-monatige Kleinkinder einsetzen, um die visuelle Aufmerksamkeit Anderer auf ein Zielobjekt zu lenken. Hierzu nutzte ich ein Studiendesign, in dem die Probanden Belohnungen von einem menschlichen Experimentator einfordern sollten. Dabei variierten sowohl die visuelle Aufmerksamkeit des Experimentators (*zugewandt* vs. *abgewandt*) als auch die Position der Belohnung (auf *der selben Seite* einer Trennwand wie der Experimentator vs. auf *der anderen Seite* der Trennwand). Sowohl Menschenaffen als auch Kleinkinder passten ihre Kommunikation an die Aufmerksamkeit des Experimentators sowie die Position der Belohnung an. Dabei positionierten sich Kleinkinder häufig im Sichtfeld des Experimentators und zeigten von dort auf die Belohnung jenseits der Wand. Affen hingegen positionierten sich entweder im Sichtfeld des Experimentators und zeigten auf diesen selbst, oder sie positionierten sich außerhalb seines Sichtfeldes in unmittelbarer Nähe zur Belohnung und zeigten auf diese. Ferner berücksichtigten beim Zeigen auf die andere Seite nur die Kinder, aber nicht die Affen, ob der Experimentator ihnen zu- oder abgewandt war. Diese Ergebnisse deuten darauf hin, dass dem Zeigen von Kleinkindern im Vorsprachalter und Menschenaffen unterschiedliche kommunikative Strategien und kognitive Mechanismen zugrunde liegen.

In Studie 3 untersuchte ich, was Schimpansen und 5 ½ jährige Kinder über die Fehlannahmen Anderer verstehen. Wie man es auch für Kinder jünger als 4 Jahre vermutet, könnte das bisherige Scheitern von Schimpansen in vergleichbaren Studien in deren mangelnder „inhibitorischer Kontrolle“ begründet liegen (anstatt einem Mangel an Kompetenz). Daher entwickelte ich zwei neuartige Paradigmen, die das Vermögen testen sollten, fremde Fehlannahmen zu erkennen, ohne dass die Probanden dabei eine stark präferierte Entscheidungsmöglichkeit inhibieren mussten. Hierzu setzte ich das Grundparadigma von Kaminski et al. (2008) ein, in dem die Probanden mit einem Artgenossen um versteckte Belohnungen konkurrierten. Dabei beobachteten die Probanden zunächst eine Reihe von Manipulationen an den Belohnungsverstecken, die der Gegenspieler je nach experimenteller Bedingung vollständig, nur teilweise oder gar nicht zu sehen bekam. Schließlich traf der Kontrahent—von den Probanden unbeobachtet—eine Wahl zwischen den alternativen Verstecken. Da die Probanden nicht in die Wahl des Kontrahenten eingeweiht waren, mussten sie, um erfolgreich zu sein, ihre Entscheidung auf Grundlage dessen treffen, was der Kontrahent gesehen hatte und was nicht. In der entscheidenden Versuchsbedingung des ersten Experiments („präferenzlose Wahl“), wussten die Probanden, dass die Verstecke dieselbe Anzahl an Belohnungen enthielten. Ihr Kontrahent hingegen nahm fälschlicherweise an, dass sich in einem Versteck eine größere Menge Belohnung befände. In der kritischen Versuchsbedingung des zweiten Experiments („unwissende Wahl“), wussten die Probanden zwar selbst nicht wo sich die Belohnung befand, beobachteten aber wie—ungesehen vom Kontrahenten—die Position der Behälter vertauscht wurde. Eine Analyse des Entscheidungsverhaltens zeigte, dass Affen und Kinder bei der Wahl der Verstecke weder die Fehlannahmen der Konkurrenten berücksichtigten, noch was diese zuvor gesehen hatten. D. h., die modifizierten Paradigmen waren scheinbar kognitiv anspruchsvoller als vergleichbare Aufgaben. Mögliche Ursachen hierfür stellen höhere Anforderungen an das Kurzzeitgedächtnis dar (Experiment 1). Ebenso könnte es sein, dass den Probanden die Abschätzung einer gegnerischen Fehlannahme schwerer fiel, da sie nicht wussten, wo konkret der Kontrahent die Belohnung vermutete (Experiment 2).

Neuere Entwicklungs- und vergleichende Studien deuten darauf hin, dass Menschenaffen im Bereich der ToM ähnliche kognitive Kompetenzen und Limitationen aufweisen wie Kinder in einem Alter von unter 4 Jahren. So zeigen z. B. beide Gruppen eine Sensitivität gegenüber fremden Fehlannahmen in impliziten Verhaltensmaßen (z. B. Blickrichtungen), aber scheitern gleichzeitig in Aufgaben, die dieses Verständnis explizit abfragen (z. B. verbal oder anhand von Entscheidungen). Studie 3 konnte leider nicht klären, ob es sich hierbei um ein Problem mangelnder Kompetenz oder Performanz handelt, da sich die beiden modifizierten Paradigmen als kognitiv anspruchsvoller als vergleichbare Studien herausstellten (und nicht als einfacher, wie ursprünglich beabsichtigt). Obwohl vieles darauf hindeutet, dass Menschenaffen und Menschen ein evolutionär ursprüngliches „ToM-Modul" miteinander teilen, zeigen die Ergebnisse meiner Dissertation auch Unterschiede auf. So deutet Studie 1 darauf hin, dass sich das Verständnis fremder visueller Wahrnehmungen vermutlich evolutionär schrittweise weiterentwickelte—von einfacheren Formen bei Orang-Utans hin zu komplexeren bei Schimpansen und Menschen. Studie 2 zeigte, dass Menschenaffen weniger geschickt darin sind, den Aufmerksamkeitsfokus Anderer per Zeigen auf ein in der Ferne gelegenes Ziel zu lenken, als menschliche Kleinkinder. Diese Unterschiede im Kommunikationsverhalten führen vermutlich dazu, dass Affen seltener Episoden geteilter Aufmerksamkeit initiieren als Kinder. Wie bereits erwähnt, scheint das Teilen unterschiedlicher Perspektiven auf ein und denselben Gegenstand eine entscheidende Erfahrungsgrundlage für das Verständnis zu liefern, dass Wahrnehmungen subjektiv sind (Moll & Meltzoff, 2012). Daher könnten die Unterschiede im Kommunikationsverhalten auch eine Erklärung dafür sein, dass Menschenaffen Probleme damit haben, fremde Fehlannahmen zu erkennen und zu verstehen, *wie* Objekte von Anderen wahrgenommen werden. Insgesamt scheinen die Erkenntnisse aus Affenstudien die Annahme der „zwei-System-Hypothese" der menschlichen ToM Entwicklung zu bestätigen. Diese Theorie postuliert ein evolutionär ursprüngliches, ontogenetisch frühzeitig entwickeltes, effizientes und unflexibles ToM-Modul, das dazu in der Lage ist, einfache Bewusstseinsvorgänge automatisch nachzuvollziehen (z. B. wo jemand zuletzt ein Objekt gesehen hat). Unter dem Einfluss von Sprache und reifender inhibitorischer Kontrolle erwerben Kinder im Alter von ungefähr 4 Jahren ein zweites, flexibleres System, das es ihnen ermöglicht, explizite Überlegungen über die Bewusstseinsvorgänge Anderer anzustellen. Dieses zweite System, das Menschenaffen zu fehlen scheint, schließt das konzeptuelle Verständnis mit ein, dass ein und derselbe Gegenstand in Abhängigkeit von der jeweiligen subjektiven Perspektive auf unterschiedliche Arten wahrgenommen werden kann.

8. References

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Appendix

Table A.1.

Sex, Age, and Warm-Up Performance of Participants

Name	Sex	Approx. age	Warm-up success
Ari	Male	7.5	Session 2
Cabang	Female	8.5	Session 1
Claire	Female	9.5	Session 1
Edwin	Male	8.5	Session 1
Eric[a]	Male	7.5	–
Galih	Male	7.5	Session 1
Imas	Female	7.5	Session 2
Jill[a]	Male	6.0	–
Kraba	Female	10.0	Session 1
Lanang	Male	8.5	Session 1
Maxene[a]	Female	8.5	–
Mercedes	Female	9.5	Session 1
Noni	Female	12.0	Session 1
Osborne	Female	9.0	Session 2
Rowland	Male	7.5	Session 1
Sallie	Female	10.0	Session 2
Yoris[a]	Male	8.5	–

[a] did not pass the pretest criterion

Table B.1.

Definition of Communicative Behaviours

Signal type	Infants	Apes	Definition
Visual			
Offer		17 (8)	Transfer of an object through the transparent barrier
Empty hands	5 (1)		Presenting one or both hands with arms bent and palms up
Point	77 (18)	1442 (32)	Goal directed extension of one (or more) finger(s) with an accompanying arm movement (including insertion of fingers through the holes in the transparent barrier)
Raise arm	1 (1)		Upwards lifting of one (or both) arm(s)
Reach	29 (11)		Goal directed arm movement with an open hand (without finger extension)
Request		27 (13)	Pressing the mouth against or cupping a hand before a hole of the transparent barrier
Shake hand		38 (7)	Repeated shaking of one (or both) hand(s)
Shake head	2 (2)	18 (5)	Repeated moving of the head from side to side or up and down
Shrug	2 (2)		Rapid lifting or contraction of the shoulders
Auditory			
Body slap	3 (2)	2 (2)	Noisily hitting one’s own body
Clap		10 (3)	Slapping hands or feet together
Jump		3 (2)	Jumping with both feet of the ground
Bang	29 (9)	127 (23)	hitting, kicking, knocking, pushing or shaking an item (barrier, wall or ground) such that a noise is produced
Spit		7 (3)	Spitting through the panel
Vocalization	256 (21)	17 (5)	Production of vocal sounds

Note. Summarizing all sessions, the columns ‘infants’ and ‘apes’ show the total number of occurrences (first number) and the number of individuals that used the respective signal (second number, in brackets).

Table B.2.

GLMM Analysis of Number of Switches to the Experimenter's Side

	Model coefficients			Likelihood ratio tests		
	Estimate	SE	*p*	χ^2	*df*	*p*
Human, Great Apes						
Intercept	-1.40	0.27	< .001			
Trial	-0.02	0.08	.808			
Sex male	0.04	0.23	.847			
Species ape	0.53	0.26	.038			
Orientation towards	0.32	0.15	.031			
Location same	-0.67	0.25	.008			
Species x Orientation				0.09	1	.771
Species x Location				0.10	1	.752
Orientation x Location	-0.61	0.26	.021	5.43	1	.020
Species x Orientation x Location				3.45	1	.063
Test variables overall:				48.16	7	< .001
Homo, Pan						
Intercept	-1.30	0.26	< .001			
Trial	0.04	0.08	.603			
Sex male	0.00	0.23	.992			
Species ape	0.65	0.25	.009			
Orientation towards	0.30	0.16	.061			
Location same	-0.49	0.25	.045			
Species x Orientation				0.18	1	.674
Species x Location				< 0.01	1	.970
Orientation x Location	-0.64	0.28	.021	5.63	1	.018
Species x Orientation x Location				3.82	1	.051
Test variables overall:				40.81	7	< .001

Table B.3.

GLMM Analysis of Number of Switches to the Other Side

	Model coefficients			Likelihood ratio tests		
	Estimate	SE	*p*	χ^2	*df*	*p*
Human, Great Apes						
Intercept	-1.28	0.29	< .001			
Trial	0.05	0.09	.593			
Sex male	0.18	0.27	.499			
Species ape	0.01	0.28	.959			
Orientation towards	0.21	0.16	.201			
Location same	0.03	0.17	.855			
Species x Orientation				3.23	1	.072
Species x Location				0.19	1	.663
Orientation x Location	-0.60	0.25	.015	6.19	1	.013
Species x Orientation x Location				2.09	1	.148
Test variables overall:				15.93	7	.026
Homo, Pan						
Intercept	-1.14	0.28	< .001			
Trial	0.08	0.09	.397			
Sex male	0.08	0.26	.753			
Species ape	0.20	0.27	.471			
Orientation towards	0.20	0.17	.248			
Location same	-0.03	0.18	.862			
Species x Orientation				3.07	1	.080
Species x Location				0.34	1	.561
Orientation x Location	-0.54	0.26	.039	4.57	1	.032
Species x Orientation x Location				1.80	1	.179
Test variables overall:				14.97	7	.036

Table B.4.

GLMM Analysis of the Number of Auditory Signals Produced at the Experimenter's Side

	Model coefficients			Likelihood ratio tests		
	Estimate	SE	*p*	χ^2	*df*	*p*
Human, Great Apes						
Intercept	-0.86	0.32	.006			
Trial	-0.19	0.12	.106			
Sex male	0.20	0.34	.563			
Species ape	-2.67	0.40	< .001			
Orientation towards	0.34	0.20	.098			
Location same	0.04	0.24	.862			
Species x Orientation				0.28	1	.594
Species x Location	1.51	0.39	< .001	13.84	1	< .001
Orientation x Location				0.20	1	.651
Species x Orientation x Location				0.32	1	.574
Test variables overall:				53.45	7	< .001
Homo, Pan						
Intercept	-0.87	0.33	.009			
Trial	-0.14	0.12	.255			
Sex male	0.20	0.36	.578			
Species ape	-2.63	0.44	< .001			
Orientation towards	0.45	0.20	.029			
Location same	0.04	0.26	.884			
Species x Orientation				< 0.01	1	.956
Species x Location	1.55	0.44	< .001	11.78	1	< .001
Orientation x Location				0.07	1	.789
Species x Orientation x Location				0.12	1	.732
Test variables overall:				45.38	7	< .001

Table B.5.

GLMM Analysis of the Number of Auditory Signals Produced at the Other Side

	Model coefficients			Likelihood ratio tests		
	Estimate	SE	*p*	χ^2	*df*	*p*
Human, Great Apes						
Intercept	-1.10	0.41	.007			
Trial	0.08	0.17	.632			
Sex male	0.09	0.40	.815			
Species ape	-1.33	0.46	.004			
Orientation towards	0.25	0.28	.376			
Location same	-4.09	1.95	.036			
Species x Orientation	-0.98	0.46	.033	3.89	1	.048
Species x Location				3.77	1	.052
Orientation x Location				0.11	1	.735
Species x Orientation x Location				2.08	1	.149
Test variables overall:				64.68	7	< .001
Homo, Pan						
Intercept	-1.04	0.42	.013			
Trial	0.05	0.19	.786			
Sex male	0.12	0.42	.773			
Species ape	-1.61	0.45	< .001			
Orientation towards	-0.04	0.27	.886			
Location same	-3.23	1.52	.033			
Species x Orientation				2.51	1	.113
Species x Location				3.11	1	.078
Orientation x Location				0.08	1	.771
Species x Orientation x Location				2.33	1	.127
Test variables overall:				50.23	7	< .001

Table B.6.

GLMM Analysis of the Number of Visual Gestures Produced at the Experimenter's Side

	Model coefficients			Likelihood ratio tests		
	Estimate	SE	*p*	χ^2	*df*	*p*
Human, Great Apes						
Intercept	-1.62	0.3	< .001			
Trial	0.00	0.05	.960			
Sex male	-0.29	0.27	.297			
Species ape	0.27	0.31	.381			
Orientation towards	1.07	0.13	< .001			
Location same	0.27	0.27	.316			
Species x Orientation				0.72	1	.397
Species x Location	1.39	0.31	< .001	20.39	1	< .001
Orientation x Location				0.46	1	.499
Species x Orientation x Location				0.41	1	.520
Test variables overall:				103.85	7	< .001
Homo, Pan						
Intercept	-1.72	0.30	< .001			
Trial	-0.04	0.07	.521			
Sex male	-0.25	0.28	.359			
Species ape	0.41	0.31	.181			
Orientation towards	1.17	0.14	< .001			
Location same	0.26	0.27	.346			
Species x Orientation				1.88	1	.170
Species x Location	1.36	0.33	< .001	18.17	1	< .001
Orientation x Location				1.62	1	.203
Species x Orientation x Location				0.13	1	.723
Test variables overall:				84.31	7	< .001

Table B.7.

GLMM Analysis of the Number of Visual Gestures Produced at the Other Side

	Model coefficients			Likelihood ratio tests		
	Estimate	SE	*p*	χ^2	*df*	*p*
Human, Great Apes						
Intercept	-1.78	0.35	< .001			
Trial	-0.05	0.09	.572			
Sex male	-0.26	0.30	.392			
Species ape	1.83	0.35	< .001			
Orientation towards	0.15	0.13	.253			
Location same	-3.17	0.65	< .001			
Species x Orientation				0.11	1	.744
Species x Location				1.23	1	.267
Orientation x Location	-1.89	0.57	.001	14.41	1	< .001
Species x Orientation x Location				0.96	1	.328
Test variables overall:				124.97	7	< .001
Homo, Pan						
Intercept	-1.89	0.37	< .001			
Trial	-0.16	0.1	.109			
Sex male	-0.22	0.33	.501			
Species ape	2.02	0.37	< .001			
Orientation towards	0.20	0.15	.182			
Location same	-3.29	0.75	< .001			
Species x Orientation				0.23	1	.635
Species x Location				1.70	1	.192
Orientation x Location	-1.49	0.61	.014	6.66	1	.010
Species x Orientation x Location				0.46	1	.499
Test variables overall:				105.39	7	< .001

Table B.8.

GLMM Analysis of the Number of Pointing Gestures Directed to the Experimenter's Side

	Model coefficients			Likelihood ratio tests		
	Estimate	SE	*p*	χ^2	*df*	*p*
Human, Great Apes						
Intercept	-3.02	0.30	< .001			
Trial	-0.01	0.05	.781			
Sex male	-0.41	0.25	.096			
Species ape	1.99	0.28	< .001			
Orientation towards	1.04	0.12	< .001			
Location same	1.40	0.12	< .001			
Species x Orientation				1.07	1	.300
Species x Location				0.20	1	.656
Orientation x Location				2.01	1	.156
Species x Orientation x Location				0.24	1	.625
Test variables overall:				122.17	7	< .001
Homo, Pan						
Intercept	-3.15	0.32	< .001			
Trial	-0.05	0.07	.491			
Sex male	-0.48	0.27	.079			
Species ape	2.13	0.30	< .001			
Orientation towards	1.14	0.14	< .001			
Location same	1.45	0.14	< .001			
Species x Orientation				1.91	1	.166
Species x Location				0.37	1	.544
Orientation x Location				1.22	1	.269
Species x Orientation x Location				0.20	1	.652
Test variables overall:				98.25	7	< .001

Table C.1.

Sex, Age and Role of Chimpanzee Participants

Name	Sex	Role	Approx. age
Asega	Male	Competitor	13
Baluku	Male	Participant	13
Bili	Female	Participant	13
Bwambale	Male	Participant	12
Ikuru*	Female	Competitor	16
Indi	Male	Participant	12
Kalema	Male	Participant	1.5
Kisembo	Male	Participant	12
Mawa	Male	Competitor	15
Namukisa	Female	Participant	12
Nkuumwa	Female	Participant	15
Okech	Male	Participant	10
Pasa	Female	Participant	12
Umutama	Male	Participant	15
Yoyo	Female	Participant	12

* participated only in Study 2

Table C.2.

Apparatus Measurements

Item	Chimpanzees	Children
main-board cups	base area Ø = 9.5 cm	base area: 13 cm *10 cm
	height: 9.5 cm	height: 7cm
opt-out cup	base area Ø = 9.5 cm	base area Ø = 9 cm
	height: 8.5 cm	height: 9 cm
sliding board	70 cm * 10 cm	61 cm * 19 cm
small-IG-blind	82 cm* 25 cm	78 cm * 29.5 cm
normal blind	front height:76cm	curtain height: 84cm
	front width: 71 cm	curtain width: 100cm
	side height: 76m	
	side width: 30m	
distance participant-competitor	≈ 1m	≈ 1m

Table C.3.

GLMM Analysis of Chimpanzees' Ratio of HQ Cup Choice

	Model coefficients			Likelihood ratio tests		
	Estimate	SE	*p*	χ^2	*df*	*p*
Intercept	0.00	0.21	.989			
Sex male	0.08	0.17	.649			
Type remove	-0.37	0.17	.030			
Condition PI	0.14	0.24	.554			
Condition MI	-0.20	0.24	.404			
Condition FI	0.06	0.24	.813			
Test variables overall:				14.38	7	.045

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Eigenständigkeitserklärung

Hiermit versichere ich, Heinz Gretscher, geboren am 10.02.1978 in Saarouis (Deutschland), die vorliegende Dissertation selbstständig verfasst und keine anderen als die angegebenen Quellen oder Hilfsmittel verwendet zu haben. Die aus fremden Quellen direkt oder indirekt übernommenen Ideen habe ich als solche kenntlich gemacht. Die Dissertation wurde—weder vollständig noch teilweise—im Rahmen eines früheren Promotionsverfahren vorgelegt oder veröffentlicht.

Ort, Datum *Heinz Gretscher*