The Role of Past Interactions in Great Apes' Communication About Absent Entities

Manuel Bohn[a], Josep Call[a,b], Michael Tomasello[a]

[a] Department of Developmental and Comparative Psychology, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany

[b] School of Psychology & Neuroscience, University of St. Andrews, St. Andrews, Fife KY16 9JP, UK

Running head: PAST INTERACTIONS IN APE COMMUNICATION

Please address correspondence to:
Manuel Bohn
Department of Developmental and Comparative Psychology
Max Planck Institute for Evolutionary Anthropology
Deutscher Platz 6
D-04103 Leipzig
Tel: +49 (0) 341 3550 438
E-mail address: manuel_bohn@eva.mpg.de

Acknowledgements

We thank S. Schütte, M. Thiele, D. Martin, K. Körfer and N. Haack for help with the data collection, R. Mundry for statistical advice, M. Schreiber for preparing the graphs and S. Kaufhold for reliability coding. We especially thank the animal caretakers of the Wolfgang Köhler Primate Research Center for their help with the apes. M. Bohn was supported by a scholarship of the German National Academic Foundation. J. Call was supported by the "SOMICS" ERC-Synergy grant (nr. 609819).

Abstract

Recent evidence suggests that great apes can use the former location of an entity to communicate about it. In this study we built on these findings to investigate the social cognitive foundations of great apes' communicative abilities. We tested whether great apes (n = 35) would adjust their requests for absent entities to previous interactions they had with their interlocutor. We manipulated the apes' experience with respect to the interlocutor's knowledge about the previous content of the now empty location, as well as their experience with the interlocutor's competence to provide additional food items. We found that apes adjusted their requests to both of these aspects but failed to integrate them with one another. These results demonstrate a surprising amount of flexibility in great apes' communicative abilities while at the same time suggesting some important limitations in their social communicative skills.

Keywords: communication; common ground; displacement; social cognition; great apes

Introduction

Communication is a social endeavour. Human communication is a social-*cognitive* endeavour in that humans interpret and produce signals in the light of the common ground they share with their interlocutor (Clark, 1996; Sperber & Wilson, 2001; Tomasello, 2008). This way of communicating enables a great deal of flexibility but it entails a considerable degree of cognitive complexity. For example, by pointing to an empty red chair one could communicate such diverse things as "This is the colour I want for my kitchen table" or "Where did Petra go?". In order to ask about the whereabouts of Petra the pointer has to consider whether the receiver knows that somebody was sitting on the chair a minute ago as well as whether she knows that the pointer is looking for someone. This information has to be part of the common ground between the interlocutors to make the pointing gesture meaningful. To form common ground, interlocutors have to interact with one another. On the basis of these interactions humans attribute psychological states such as knowledge, beliefs or competencies to one another and subsequently consider them in communicative interactions.

Human infants engage in communicative interactions that suggest sensitivity to common ground from their first birthday onwards. They interpret ambiguous verbal utterances or pointing gestures depending on how they interacted with the speaker before (Liebal, Behne, Carpenter, & Tomasello, 2009; Moll & Tomasello, 2007; Saylor & Ganea, 2007; Tomasello & Haberl, 2003). Slightly older children also adjust their own communicative acts to the prior interactions with their interlocutor (Liebal, Carpenter, & Tomasello, 2010). The extent to which non-human animals also rely on common ground for communication is often debated (Leavens et al., 2015; Moore, 2013; Scott-Phillips, 2015b; Tomasello, 2008) but rarely addressed empirically.

Common ground is one source that specifies the intended referent of an utterance and it is therefore important in the discussion whether animal signals have (non-natural) meaning in the same way as human signals do (Grice, 1957; Hobaiter & Byrne, 2014; Moore, 2015; Scott-Phillips, 2015a).

Great apes display some abilities that are important prerequisites to use common ground in communication. They are known to be flexible and intentional communicators who adapt their communication to the present social context (Call & Tomasello, 2007; Hobaiter & Byrne, 2011; Leavens, Russell, & Hopkins, 2005). During communicative interactions with conspecifics, chimpanzees adjust their gestures to the attentional state of their recipient by actively moving into the line of sight of the recipient or resorting to tactile gestures (Call & Tomasello, 2007; Liebal, Call, & Tomasello, 2004; Liebal, Call, Tomasello, & Pika, 2004). In a similar way, all great ape species prefer to beg food from a human who is attending to them (Kaminski, Call, & Tomasello, 2004; Tempelmann, Kaminski, & Liebal, 2011). Outside the realm of communication there is evidence showing that chimpanzees prefer to approach food items that a competitor cannot see or has not seen (Hare, Call, Agnetta, & Tomasello, 2000; Hare, Call, & Tomasello, 2001; Karg, Schmelz, Call, & Tomasello, 2015) suggesting that they expect their competitor to act based on what she sees or has seen in the immediate past. However, the question is whether great apes adjust their own communication depending on what the partner has seen in the immediate past. Recent evidence suggets that this indeed the case. Crockford and colleagues (2012) found that wild chimpanzees emitted alarm calls depending on whether or not they witnessed group members receiving information about the presence of a predator.

All the studies reported above are concerned with tracking interactions that happened in the immediate past. What about information about others derived from long term interactions? Woodruff and Premack (1979) confronted chimpanzees with two humans who would, when informed about hidden food, either hand it over to the subject (cooperative) or take it away (competitive). The competitive human wore a distinct outfit and behaved in a hostile way toward the chimpanzees outside the experiment. Subjects initially failed to withhold information from the competitive human but eventually learned to do so after a substantial amount of training. However, the long training period suggests that, instead of ascribing enduring characteristics to a person, subjects learned to inhibit communication in the presence of a human wearing the competitive outfit.

To sum up, there is ample evidence that great apes adjust their behavior to their partner's psychological states (e.g. seeing or knowing). Furthermore, there is at least some evidence apes adjust their own communication to these psychological states if they are the consequence of a relatively recent interaction. However, it is not clear if they are able to take into account characteristics of others deduced from more distant interactions with them. Furthermore, to our knowledge, there is no study that has systematically investigated if great apes are able to integrate two different psychological states of another individual in a communicative interaction.

A powerful way to investigate the role of common ground in non-linguistic communication is by studying pointing to absent entities. Language-trained apes have been reported to use tokens, lexigrams or gestures to refer to absent referents (e.g. Gardner, Gardner, & Van Cantfort, 1989; Premack & Premack, 1983; Savage-Rumbaugh, McDonald, Sevcik, Hopkins, & Rubert, 1986) and to point to occluded objects (Menzel, 1999; Roberts, Vick, Roberts, & Menzel, 2014). However, in the case of pointing to absent entities, the referent is not present, neither visible nor occluded, in the moment it is communicated about (see also Lyn et al., 2014 for this distinction). The interlocutors have to rely on past interactions in which both of them jointly witnessed the presence of the referent. Recently, Liszkowski, Schäfer, Carpenter, and Tomasello (2009) tested whether 12-month old human infants and chimpanzees use pointing to communicate about absent entities. In this study, the non-verbal subjects had the opportunity to point to the previous location of a now absent object to request more of it. The underlying assumption was that doing so requires the subject to keep track of the relevant common ground, in this case the former content of the location, they share with the individual they request from. Whereas this study found that only human infants communicate about absent entities, two subsequent studies found that apes do so as well (Bohn, Call, & Tomasello, 2015; Lyn et al., 2014). However, even though these studies rely on it for the explanation of their results, none of them investigated common ground or its prerequisites directly. It is unclear whether apes base their communicative acts on the psychological states they attribute to others as a consequence of interacting with them. For example, in a situation as described above, apes should refrain from pointing to the empty location in a situation in which their interlocutor doesn’t know about the former content of the location. Or they should not point in a situation in which the interlocutor lacks the competence to provide additional objects.

To address these issues, we modified the methodology established by Bohn et al. (2015). They presented subjects with two plates from which apes could request food items by pointing. The type of food presented in both plates was either of the same quality (both high quality: HQ or both low quality: LQ) or of different quality (one HQ and one LQ). During test trials, one plate still contained food while all items from the other plate had already been requested. In general, subjects preferred to point to the remaining visible food items instead of the empty plate. More importantly however, whenever subjects pointed to the empty plate they did so in a highly systematic way. Apes ignored the otherwise desirable visible food item and pointed to the empty plate only when the visible food item was of lower quality compared to the absent items. This result showed that apes requested *specific* absent entities. We adjusted this procedure to test whether apes would further adjust their communication about absent entities to the knowledge and competence of their interlocutor. Even though this setup does not allow us to investigate full-blown common ground (i.e. the sharedness of the psychological states in question)–it tests whether apes consider the necessary prerequisites to form common ground and thereby allows us to determine the evolutionary origins of the ability in question.

We presented apes with two plates containing food items of different quality. As soon as all items from one plate were requested, the experimenter left the room and, after a short delay, the same or a different experimenter returned. To investigate the role of the experimenter's knowledge we tested whether apes would point to the empty plate differently depending on whether or not the returning experimenter had seen what was on the plate previously (predictor: *see*). To investigate the role of the experimenter's competence, we tested whether apes would point to the empty plate differently depending on whether the experimenter did or did not bring additional food items in an earlier interaction (predictor: *bring*). If apes would consider both of these predictors, this would be good evidence that they evaluate the prior interactions with the experimenter for their relevance in the on-going communicative interaction. This in turn would suggest that some important prerequisites to form common ground are evolutionary ancient. Furthermore, by varying the experimenter's knowledge and competence at the same time, we were able to investigate whether apes are able to integrate different aspects of previous interactions.

Method

Subjects

We tested 35 non-human great apes (*Gorilla gorilla, Pan troglodytes, Pongo abelii, Pan paniscus*) housed at the Wolfgang Köhler Primate Research Center at Zoo Leipzig, Germany. All apes participated in an earlier study using the same setup (Bohn et al., 2015). Four apes completed only parts of the experiment (see Table S1 in the supplemental material). Participation was voluntary, apes were never food deprived and water was available ad libitum throughout the experiment. Research was non-invasive and strictly adhered to the legal requirements of Germany. Animal husbandry and research complied with the EAZA Minimum Standards for the Accommodation and Care of Animals in Zoos and Aquaria and the WAZA Ethical Guidelines for the Conduct of Research on Animals by Zoos and Aquarium.

Setup

Apes were presented with two identical plates on a table in front of a Plexiglas window (see Figure 1). They could request food items placed on these plates one by one from an experimenter seated on the other side of the table by pointing with their finger through a hole in front of the respective plate. The experimenter handed the items over through a third hole in the middle of the panel.

--- *Insert Figure 1* ---

Procedure

Each session comprised two phases, the warm-up phase and the test phase (see Figure 1). During the warm-up phase both plates were baited with three food items on each plate. As soon as the subject requested all food items from one plate, the experimenter left the room. After a ten second delay the test phase began with the return of an experimenter. During the test phase, one plate contained food items whereas the other was empty. Subjects were allowed to request further items by either pointing to the plate containing food or the empty plate. The session ended if the subject a) pointed to the empty plate, b) requested all remaining visible food items or c) did not point for 90s. If the subject pointed to the empty plate, the experimenter left the room and retrieved one more item of the kind that was previously on that plate. The maximum number of points per session was one for the empty plate and three for the visible alternative.

Following Bohn et al. (2015) there were two different conditions with respect to the baiting of the plates. In the *same* condition, both plates contained the same food type (HQ = grapes or LQ-= pieces of apple or carrot) and in the *different* condition the plates contained different food types (one HQ and the other LQ) resulting in 4 different constellations (Table S2 in supplemental material shows the different baiting constellations). We made sure that the LQ food was desirable for the apes when presented on its own. If apes were specific in their requests for absent entities, they should point to the empty plate more often in the *different* condition (Bohn et al., 2015).

All apes participated in another study comprising the same setup and the same E1 immediately prior to the current experiment (Bohn et al., 2015). In this study E1 repeatedly re-baited the plates with food and thereby demonstrated that he was able to bring new food items. However, apes were never trained to point to empty plates during this study. We introduced a novel E2 with whom apes never interacted in a similar way before (see supplemental material for details). If the same experimenter returned in the test phase as was present in the warm-up phase she had seen the food on the now empty plate: *see*(+), if a different experimenter returned she had not: *see*(-). If the returning experimenter was E1, he had demonstrated his ability to bring more food before: *bring*(+), if it was E2, she had not: *bring*(-). This resulted in four different configurations (see Figure 1). For each of these configurations, each subject received one session in the *same* condition and one session in the *different* condition, resulting in eight test sessions per individual. For each unique combination of condition and configuration, subjects received only a single test session.

The order of sessions was counterbalanced across subjects. Due to a two-month hiatus half way through the study apes received additional training sessions before the second half of the experiment. In these training sessions apes requested food items presented on a single plate from E1 who re-baited the plate multiple times with the same kind of food. Importantly, subjects were never rewarded for pointing to an empty plate during training sessions (see supplemental material for details on counterbalancing and the training procedure).

In order to point to the empty plate apes had to disregard an otherwise desirable food item. We therefore expected a rather low rate of pointing to empty plates. However, this alternative option is crucial to draw conclusions about the psychological processes underlying subjects' behaviour. In the absence of an alternative, apes might consider the relevant aspects of prior interactions with the experimenter but point to the empty plate nevertheless, simply because they have nothing else to do (see Bohn et al., 2015 for theoretical and empirical support for the necessity of an alternative option).

Coding and analysis

For each trial in the test-phase we coded whether subjects pointed or not, through which hole the subject pointed and whether the subject requested absent food items or not. We defined pointing in the following way: the subject inserted one or more fingers into *one* of the holes in the Plexiglas panel so that they protruded on the other side. We did not code as pointing if the subject simultaneously inserted fingers into more than one hole at the same time or if subjects inserted a finger while E was not present. A second coder, blind to the purpose of the study, coded a random selection of 25% of test-trials. There was a very high agreement of 98.81% between the two coders ($\kappa = .98$).

We used generalized linear mixed models (GLMM) with a binomial error structure to analyse if the binary response (point to absent or not) was influenced by condition and the different configurations. All models were fitted in R (R Core Team, 2012) using the function *glmer* of the R-package *lme4* (Bates, Maechler, & Bolker, 2012). We used likelihood ratio tests (LRT) to assess whether the inclusion of predictors and their interactions improved the general fit of a model to the data by comparing models with and without the respective effects (Dobson & Barnett, 2008). All models comprised subject ID as a random effect to account for repeated testing of the same individuals.

Results

We observed a total number of 665 points during test sessions. 639 points were directed at visible food items and 26 points were directed at the empty plates. As expected, the rate of pointing to empty plates was low because apes chose the visible alternative instead (see Bohn et al., 2015 for similar results and supplemental material for details). Nevertheless, we observed a sufficient number of points to empty plates to investigate whether they were influenced by the experimental manipulations. Points to the empty plate were distributed in the following way: 18 points occurred in the *different* condition, 16 of which were directed at the plate that previously contained HQ food items. Eight occurred in the *same* condition, five of which in sessions with LQ food on both sides. The number of points to empty plates did not increase across test sessions. On the contrary, it decreased across test sessions (see supplemental material for details). Figure 2 shows how these points were distributed across the different configurations. In trials in which apes did not point to the empty plate they pointed to the visible alternative in 99% of trials when E1 had returned and in 97% of trials when E2 had returned. There was no significant difference in the rate of pointing in general between E1 and E2 (Wilcoxon signed ranks test, $T^{+} = 253.5$, $p = .12$).

--- Insert Figure 2 ---

A model comprising condition as a fixed within subject effect fitted the data significantly better compared to a null model lacking it (LRT: $\chi^2(1) = 4.54$, $p = .033$; GLMM estimate: $\beta = 0.99$, 95% CI = [0.08: 2.00]). Apes pointed to the empty plate more often in the *different* than in the *same* condition. This finding replicates the result of Bohn et al. (2015) and adds to evidence that apes' points to empty plates follow a systematic pattern. The inclusion of sex, species and session as fixed effects did not improve the model fit significantly and these predictors were therefore dropped for the subsequent analysis (LRT: $\chi^2(5) = 5.28$, $p > .250$). To determine whether the previous interactions with the experimenter further influenced apes' pointing to empty plates we added *see, bring* and the interactions with condition up to the third order as fixed within subject effects. Inclusion of these predictors significantly improved the model fit compared to the model only comprising condition (LRT: $\chi^2(6) = 22.14$, $p = .001$). This result shows that apes' requests for absent entities were influenced by the previous interactions with the experimenter.

Subsequently, we investigated the contribution of *see* and *bring* to this result in more detail by looking at the three-way interaction between condition, *see* and *bring*. This interaction was not significant (LRT: $\chi^2(1) = 0.37$, $p > .250$). We therefore removed the three-way interaction and looked at the two-way interactions among condition, *see* and *bring*. We found a significant interaction between condition and *bring* (LRT: $\chi^2(1) = 5.49$, $p = .019$; GLMM estimate: $\beta = 2.62$, 95% CI = [0.44: 5.08]). Apes pointed more often to an empty plate in the *different* condition if the returning experimenter provided additional food items in previous interactions. In contrast, we found no effect of the interactions between condition and *see* (LRT: $\chi^2(1) = 0.05$, $p > .250$) or *see* and *bring* (LRT: $\chi^2(1) = 0.02$, $p > .250$). After excluding the non-significant two-way interactions we found a main effect of *see* (LRT: $\chi^2(1) = 4.97$, $p = .026$; GLMM estimate: $\beta = 1.12$, 95% CI = [0.13: 2.24]). Apes pointed more often to an empty plate if the experimenter had previously seen the content of the plate.

Discussion

Great apes flexibly adjusted their requests for absent entities depending on three factors: the previous content of a now empty plate (condition), whether the experimenter had seen the content of the now empty plate (*see*) and whether the experimenter provided additional food items in a previous interaction (*bring*). This is evidence that apes tracked the relevant aspects of previous interactions with their interlocutor and considered them when engaging in subsequent communicative interactions with him or her.

These results cannot be explained by task specific associative learning or simple heuristics. First, apes only received one test session for each combination of condition and configuration so that each subject could only contribute one point to empty plates for each of these combinations. Any association formed as a consequence of being rewarded for pointing to the empty plate could therefore not influence the result of that specific combination any further. If being rewarded for pointing to the empty plate had any effect at all, it should have increased the number of points to empty plates in subsequent test sessions regardless of combination. However, this was not the case since the number of points to empty plates decreased rather than increased in later sessions (see supplemental material for details). Second, apes did not simply associate E1 with more food as they only pointed more often for him in the *different* condition. Finally, our results cannot be explained by a general unwillingness to point for E2, since the rate of pointing in general did not differ between the E1 and E2. Taken together this suggests that apes' requests were not directly influenced by the amount and kind of food they got from each experimenter but rather by *how* they interacted with him/her previously. Next we discuss in more detail the factors that affected subjects' choices and their interpretation.

Overall, apes were specific in their requests as they requested more absent entities in the *different* condition, i.e. when the previous content of the now empty plate was of higher quality than the visible content of the other plate. This finding replicates the earlier study by Bohn et al. (2015). More importantly, we found that the type of interaction they had with the experimenter previously further modulated these specific requests. Apes requested specific absent entities more often from an experimenter (E1) who previously demonstrated his competence to provide additional food than from a novel experimenter (E2). Even if E2 had just given them HQ items in the *different* condition, they did not request additional items from her. These results show that apes communicated with a *specific* individual about *specific* absent entities. This kind of spontaneous and flexible adjustment of communicative acts to past social interactions goes beyond what has been shown in earlier studies in which chimpanzees were directly trained to inhibit and redirect communicative acts in the presence of specific individuals (Woodruff & Premack, 1979). Moreover, the differential pattern of responses suggests that apes may have ascribed a general competence to E1 (“able to bring more of what was previously on that plate”) instead of an object specific one (“able to bring grapes”). In the latter case they should not have adjusted their requests to the previous content of the plate as well and should have made more requests in the *same* condition with LQ items on both plates.

However, since we did not counterbalance the identity of E1, we cannot rule out that apes’ evaluation of E1’s ability to provide additional food items was solely based on our experimental manipulations. It is conceivable that other factors such as E1’s gender or general appearance, rather than the specific past interactions with E1, might have been responsible for the effect of *bring*. While such an alternative explanation is certainly possible, we think that it is highly unlikely that apes’ prior experiences outside the studies considered here led them to learn that only E1 (or other humans who resembled E1) would provide additional food items after pointing to their previous location. We think that it is more likely that the specific experiences with E1 during training trials and the study by Bohn et al. (2015), which involved the same setup and food items, influenced how apes communicated with E1 in the current study.

We also found that apes were more likely to point to the empty plate if the returning experimenter had seen the content of the now empty plate, regardless of his competence and condition. This result is in line with previous research showing that apes adjust their behaviour depending on whether another individual has experienced something or not (Crockford et al., 2012; Hare et al., 2001). The presence of a main effect of *see* rather than an interaction between *see* and condition reveals how subjects judged the importance of the two factors relative to one another. The general rate of pointing for absent entities for E2 – *bring*(-) – was too low to differ between the two conditions or the two levels of *see* (see Figure 2). This means that the experimenter's competence was a necessary requirement for *see* or condition to have an effect at all. This is reminiscent of apes preferentially begging from a human whose face was oriented towards them but only when that human was in a position in which she was capable of handing over food (body oriented towards the ape) (Kaminski et al., 2004). When her body was oriented away from the ape, they generally begged less from her and did not care about her face orientation anymore.

Even though we observed most points to empty plates in the *different* condition for an experimenter who was knowledgeable as well as competent, apes also requested specific absent entities from E1 when E1 had not seen the absent food before (see Figure 2). This suggests that apes did not take into account the interdependent nature of knowledge and competence. In order to use a location to request more of its previous content, it is not sufficient to know that the other person is willing and able to provide more food, *at the same time* it is necessary to know whether she knows what the location contained previously. If we are willing to see the adjustment for knowledge and competence in this study as cases of attribution of psychological states, we might conclude that apes are limited in their ability to integrate different psychological states of the same individual. This might help to explain why great ape communication among conspecifics is usually based on naturally meaningful embodied behaviours instead of more ambiguous signals that require a detailed tracking of common ground (Moore, 2013; Tomasello, 2008). However, future research should investigate if these results are specific to communicative interactions about absent entities or constitute a general limitation of great apes' social-cognitive abilities. As we highlighted in the introduction, this study did not address full-blown common ground but only its necessary prerequisites. Following studies with children (Moll, Carpenter, & Tomasello, 2007) it would be necessary to vary how apes learn about the experimenter's psychological states (in joint engagement or while eavesdropping) to determine whether they consider how psychological states come to be shared between individuals.

In sum, these results show that great apes consider relevant aspects of previous interactions with other individuals that are necessary prerequisites to form common ground with them. However, our results also suggest that apes might be limited in their ability to integrate different psychological states of an individual simultaneously. Overall, our study sheds light on the social embedding of great apes' communicative abilities and thereby helps to identify the evolutionary foundations on which human communication rests.

References

Bates, B., Maechler, M., & Bolker, B. (2012). lme4: Linear mixed-effects models using S4 classes. R package (Version 0.999999-0.).

Bohn, M., Call, J., & Tomasello, M. (2015). Communication about absent entities in great apes and human infants. *Cognition, 145*, 63-72. doi: 10.1016/j.cognition.2015.08.009

Call, J., & Tomasello, M. (2007). *The gestural communication of apes and monkeys*. New York: Lawrence Erlbaum Associates.

Clark, H. H. (1996). *Using language*. Cambridge: Cambridge University Press.

Crockford, C., Wittig, R. M., Mundry, R., & Zuberbuhler, K. (2012). Wild chimpanzees inform ignorant group members of danger. *Current Biology, 22*(2), 142-146. doi: 10.1016/j.cub.2011.11.053

Dobson, A. J., & Barnett, A. G. (2008). *An introduction to generalized linear models* (3rd ed.). Boca Raton: CRC Press.

Gardner, R. A., Gardner, B. T., & Van Cantfort, T. E. (1989). *Teaching sign language to chimpanzees*. Albany, NY: State University of New York Press.

Grice, H. P. (1957). Meaning. *Philosophical Review, 66*(3), 377-388.

Hare, B., Call, J., Agnetta, B., & Tomasello, M. (2000). Chimpanzees know what conspecifics do and do not see. *Animal Behaviour, 59*(4), 771-785. doi: 10.1006/anbe.1999.1377

Hare, B., Call, J., & Tomasello, M. (2001). Do chimpanzees know what conspecifics know? *Animal Behaviour, 61*(1), 139–151. doi: 10.1006/anbe.2000.1518 11170704

Hobaiter, C., & Byrne, R. W. (2011). The gestural repertoire of the wild chimpanzee. *Animal Cognition, 14*(5), 745-767. doi: 10.1007/s10071-011-0409-2

Hobaiter, C., & Byrne, R. W. (2014). The meanings of chimpanzee gestures. *Current Biology, 24*(14), 1596-1600. doi: 10.1016/j.cub.2014.05.066

Kaminski, J., Call, J., & Tomasello, M. (2004). Body orientation and face orientation: Two factors controlling apes' begging behavior from humans. *Animal Cognition, 7*(4), 216-223. doi: 10.1007/S10071-004-0214-2

Karg, K., Schmelz, M., Call, J., & Tomasello, M. (2015). The goggles experiment: Can chimpanzees use self-experience to infer what a competitor can see? *Animal Behaviour, 105*, 211-221. doi: 10.1016/j.anbehav.2015.04.028.

Leavens, D. A., Reamer, L. A., Mareno, M. C., Russell, J. L., Wilson, D., Schapiro, S. J., & Hopkins, W. D. (2015). Distal communication by chimpanzees (Pan troglodytes): Evidence for common ground? *Child Development, 86*(5), 1623-1638. doi: 10.1111/cdev.12404

Leavens, D. A., Russell, J. L., & Hopkins, W. D. (2005). Intentionality as measured in the persistence and elaboration of communication by chimpanzees (*Pan troglodytes*). *Child Development, 76*(1), 291-306.

Liebal, K., Behne, T., Carpenter, M., & Tomasello, M. (2009). Infants use shared experience to interpret pointing gestures. *Developmental Science, 12*(2), 264-271. doi: 10.1111/j.1467-7687.2008.00758.x

Liebal, K., Call, J., & Tomasello, M. (2004). Use of gesture sequences in chimpanzees. *American Journal of Primatology, 64*(4), 377-396. doi: 10.1002/ajp.20087

Liebal, K., Call, J., Tomasello, M., & Pika, S. (2004). To move or not to move: How apes adjust to the attentional state of others. *Interaction Studies, 5*(2), 199-219. doi: 10.1075/is.5.2.03lie

Liebal, K., Carpenter, M., & Tomasello, M. (2010). Infants' use of shared experience in declarative pointing. *Infancy, 15*(5), 545–556. doi: 10.1111/j.1532-7078.2009.00028.x

Liszkowski, U., Schäfer, M., Carpenter, M., & Tomasello, M. (2009). Prelinguistic infants, but not chimpanzees, communicate about absent entities. *Psychological Science, 20*(5), 654-660. doi: 10.1111/j.1467-9280.2009.02346.x

Lyn, H., Russell, J. L., Leavens, D. A., Bard, K. A., Boysen, S. T., Schaeffer, J. A., & Hopkins, W. D. (2014). Apes communicate about absent and displaced objects: Methodology matters. *Animal Cognition, 17*(1), 85-94. doi: 10.1007/s10071-013-0640-0

Menzel, C. R. (1999). Unprompted recall and reporting of hidden objects by a chimpanzee (Pan troglodytes) after extended delays. *Journal of Comparative Psychology, 113*(4), 426-434. doi: 10.1037/0735-7036.113.4.426 10608566

Moll, H., Carpenter, M., & Tomasello, M. (2007). Fourteen-month-olds know what others experience only in joint engagement. *Developmental Science, 10*(6), 826-835. doi: 10.1111/j.1467-7687.2007.00615.x

Moll, H., & Tomasello, M. (2007). How 14-and 18-month-olds know what others have experienced. *Developmental Psychology, 43*(2), 309-317. doi: 10.1037/0012-1649.43.2.309

Moore, R. (2013). Evidence and interpretation in great ape gestural communication. *Humana Mente, 24*, 27-51.

Moore, R. (2015). Meaning and ostension in great ape gestural communication. *Animal Cognition, 19*(1), 223-231. doi: 10.1007/s10071-015-0905-x

Premack, D., & Premack, A. J. (1983). *The mind of an ape*. New York: Norton.

R Core Team. (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Roberts, A. I., Vick, S. J., Roberts, S. G. B., & Menzel, C. R. (2014). Chimpanzees modify intentional gestures to coordinate a search for hidden food. *Nature Communications, 5*(3088). doi: 10.1038/ncomms4088

Savage-Rumbaugh, E. S., McDonald, K., Sevcik, R. A., Hopkins, W. D., & Rubert, E. (1986). Spontaneous symbol acquisition and communicative use by pygmy chimpanzees (Pan paniscus). *Journal of Experimental Psychology: General, 115*(3), 211-235. doi: 10.1037/0096-3445.115.3.211 2428917

Saylor, M. M., & Ganea, P. (2007). Infants interpret ambiguous requests for absent objects. *Developmental Psychology, 43*(3), 696-704. doi: 10.1037/0012-1649.43.3.696

Scott-Phillips, T. C. (2015a). Meaning in animal and human communication. *Animal Cognition, 18*(3), 801-805. doi: 10.1007/s10071-015-0845-5 25647173

Scott-Phillips, T. C. (2015b). *Speaking our minds: Why human communication is different, and how language evolved to make it special*. New York, NY: Palgrave Macmillan.

Sperber, D., & Wilson, D. (2001). *Relevance: Communication and cognition* (2nd ed.). Oxford ; Cambridge, MA: Blackwell Publishers.

Tempelmann, S., Kaminski, J., & Liebal, K. (2011). Focus on the essential: All great apes know when others are being attentive. *Animal Cognition, 14*(3), 433-439. doi: 10.1007/s10071-011-0378-5

Tomasello, M. (2008). *Origins of human communication*. Cambridge, MA: MIT Press.

Tomasello, M., & Haberl, K. (2003). Understanding attention: 12-and 18-month-olds know what is new for other persons. *Developmental Psychology, 39*(5), 906-912. doi: 10.1037/0012-1649.39.5.906

Woodruff, G., & Premack, D. (1979). Intentional communication in the chimpanzee - development of deception. *Cognition, 7*(4), 333-362. doi: 10.1016/0010-0277(79)90021-0

Figures an Captions

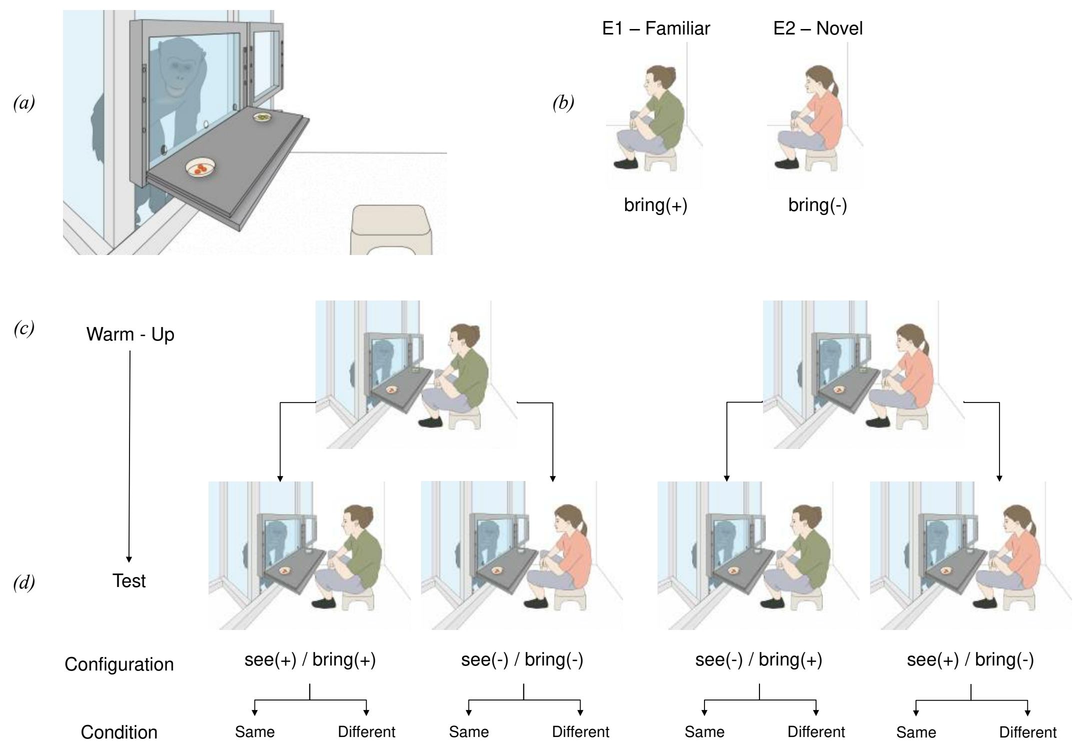

Figure 1. Schematic overview for (a) the basic setup with two baited plates, (b) the experimenters involved in the study, (c) the two different variants of the warm-up phase and (d) the resulting four different configurations in the test phase (with two different conditions per configuration). Subjects received a single test session per condition for each configuration. Subjects could request food items by pointing through the hole in front of the two plates.

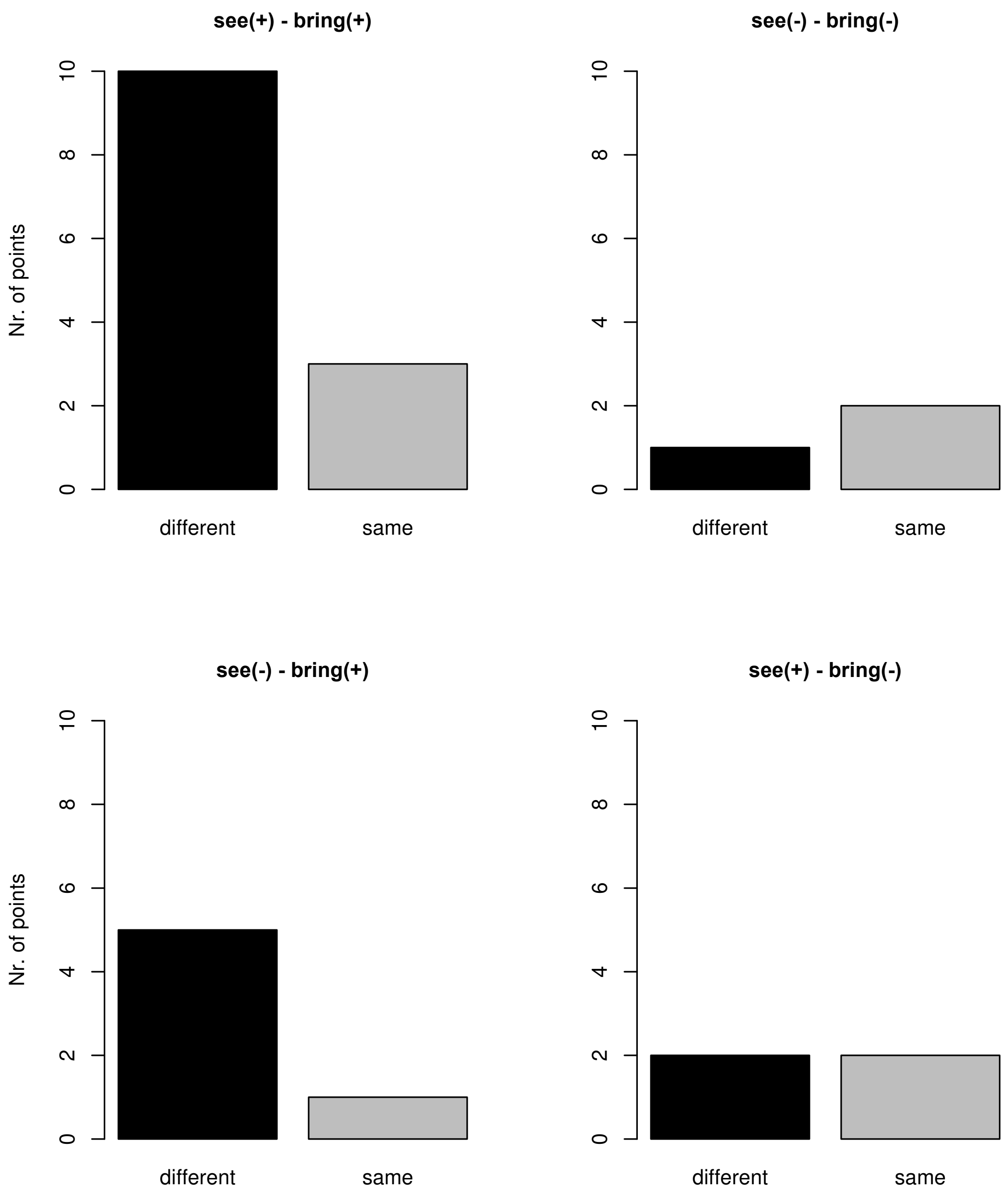

Figure 2. Number of points to empty plates per configuration and condition. Each subject received one test session per condition in each configuration.