

The development and flexibility of gaze alternations in bonobos and chimpanzees

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Abstract

Infants' early gaze alternations are one of their first steps towards a sophisticated understanding of the social world. This ability, to gaze alternate between an object of interest and another individual also attending to that object, has been considered foundational to the development of many complex social-cognitive abilities, such as theory of mind and language. However, to understand the evolution of these abilities, it is important to identify whether and how gaze alternations are used and develop in our closest living relatives, bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*). Here, we evaluated the development of gaze alternations in a large, developmental sample of bonobos ($N = 17$) and chimpanzees ($N = 35$). To assess the flexibility of ape gaze alternations, we tested whether they produced gaze alternations when requesting food from a human who was either visually attentive or visually inattentive. Similarly to human infants, both bonobos and chimpanzees produced gaze alternations, and did so more frequently when a human communicative partner was visually attentive. However, unlike humans, who gaze alternate frequently from early in development, chimpanzees did not begin to gaze alternate frequently until adulthood. Bonobos produced very few gaze alternations, regardless of age. Thus, it may be the early emergence of gaze alternations, as opposed gaze alternations themselves, that is derived in the human lineage. The distinctively early emergence of gaze alternations in humans may be a critical underpinning for the development of complex human social-cognitive abilities.

RESEARCH HIGHLIGHTS

- The developmental importance of gaze alternations in humans is well documented. However, comparative data are still needed to understand the evolutionary origins of gaze alternations.
- In a developmental sample of bonobos and chimpanzees, we tested whether individuals produced gaze alternations when requesting food from either an attentive or an inattentive experimenter.
- Individuals gaze alternated more when interacting with an attentive experimenter. Individuals produced few gaze alternations (bonobos) or frequently gaze alternated only after reaching adulthood (chimpanzees).
- These findings suggest that the distinctively early emergence of gaze alternations in humans may have evolved to support the development of complex human social-cognitive abilities.

1 | INTRODUCTION

Months before infants produce their first words, they begin to engage with others using their eyes. For instance, infants will often alternate their gaze between an object of interest and another individual (Bates, Camaioni, & Volterra, 1975; Bruner, 1982; Tomasello, 1995). As early as 10 months, infants will produce these "gaze alternations" almost exclusively when others are attentive, as opposed to inattentive (Striano & Rochat, 2000). These gaze alternations are often regarded as the "hallmark" of joint attention because they reflect infants' desire to share attention with a partner (Carpenter, Nagell, & Tomasello, 1998; Desrochers, Morissette, & Ricard, 1995; Leung & Rheingold, 1981). This has led researchers to argue that infants' gaze alternations help provide the foundation upon which more complex social-cognitive skills, such as theory of mind and language, develop



(Akhtar & Gernsbacher, 2007; Bruner, 1983; Tomasello, Carpenter, & Liszkowski, 2007).

To better understand the origins of these social-cognitive skills, researchers have tested which aspects of human social cognition are shared with our closest living nonhuman primate relatives, bonobos and chimpanzees. While very young children (i.e., 2-year-olds) do not differ from bonobos and chimpanzees in some non-social tasks, such as discriminating numerical quantities (Wobber, Herrmann, Hare, Wrangham, & Tomasello, 2013), young children consistently outperform bonobos and chimpanzees in social-cognitive tasks, such as following communicative cues to locate a hidden reward (Herrmann, Call, Hernandez-Lloreda, Hare, & Tomasello, 2007). For humans, many of these social-cognitive skills are already in place by 9–12 months (Carpenter et al., 1998), whereas the earliest evidence of these skills in chimpanzees is not present until 3 years (Tomasello, Hare, & Fogleman, 2001). Thus, not only do humans have more advanced social-cognitive skills than nonhuman primates, but they also develop them very early in development. This has led researchers to argue that the distinctively early emergence of social-cognitive skills may provide a foundation for the development of other important aspects of human cognition, such as language and culture (Herrmann et al., 2007; MacLean, 2016; Tomasello, 1999).

While previous research has demonstrated that nonhuman primates produce gaze alternations, the ontogenetic trajectory of these behaviors, and the flexibility with which they are used, are not well understood. Both experimental and observational research on captive and wild chimpanzees has revealed that gaze alternations are a recurrent part of chimpanzees' daily activities (Call & Tomasello, 1994; Leavens & Hopkins, 1998). For instance, gaze alternations are produced most frequently during communicative exchanges (e.g., food requesting contexts; Plooi, 1978) and collaborative group activities (e.g., group travel as a recruitment strategy; Gruber & Zuberbühler, 2013). An observational study on a set of five wild chimpanzees revealed that the production of gaze alternations increased across development (Tomasello, George, Kruger, Farrar, & Evans, 1985).

Whether nonhuman apes take the attentional state of their communicative partner into consideration while gaze alternating remains unknown. Relatedly, previous work has demonstrated that nonhuman apes are sensitive to the psychological states of others (i.e., are aware of what others can and cannot see; Hare, Call, & Tomasello, 2006; MacLean & Hare, 2012; Tempelmann, Kaminski, & Liebal, 2011). For instance, they produce communicative signals in the modality that is most relevant for their communicative partner. That is, they produce more visual signals when a communicative partner is only able to see them, and produce more auditory signals when a communicative partner is only able to hear them (Hostetter, Hopkins, & Cantero, 2001; Tomasello, Call, Nagell, Olguin, & Carpenter, 1994). That nonhuman apes have the requisite skills for understanding the perspectives of others when deploying visual and auditory signals suggests that they may also do so when producing gaze alternations.

Recent work with nonhuman primates more distantly related to humans, namely squirrel monkeys, has found that monkeys also produce gaze alternations (Anderson, Kuwahata, & Fujita, 2007).

Interestingly, they are most likely to gaze alternate while they are gesturing (Anderson et al., 2007), or when a communicative partner is visually attentive (Bourjade, Meguerditchian, Maille, Gaunet, & Vauclair, 2014). Together, these studies provide further evidence for the hypothesis that nonhuman apes may take the attentional state of a communicative partner into consideration while gaze alternating.

1.1 | The current study

While previous research has documented the presence of gaze alternations in nonhuman primates, these studies often relied on small sample sizes and/or a single species and setting. As a result, we know relatively little about the development of gaze alternations, the contexts in which they are produced, and whether they are produced differently across taxa. To address these questions, the current study assessed the production of gaze alternations in a large developmental sample of bonobos and chimpanzees, using a paradigm and methodology similar to studies with human infants. This paradigm measures gaze alternations between a desirable object and an experimenter who is either facing toward, or away from, the participant (as in Leavens, Russell, & Hopkins, 2010; Lucca & Wilbourn, 2016; Striano & Rochat, 2000).

By 10 months, infants show a sensitivity to an adult's attentional stance and will preferentially gaze alternate when an experimenter is attentive, compared to inattentive (Striano & Rochat, 2000). This pattern suggests that infants' gaze alternations are not simple "checking back" behaviors that allow infants to see what other individuals are doing. Rather, infants' early gaze alternations are used in intentionally communicative ways to share their attention with others. If gaze alternations provide the foundation for complex human social-cognitive abilities, then we would expect that nonhuman apes will not show this pattern, and if they do it will develop in a trajectory that is later-emerging than that seen in humans. Alternatively, if the last common ancestor of humans and *Panins* exhibited early-emerging human-like use of gaze alternations, then bonobos and chimpanzees should also begin to gaze alternate early in development and demonstrate a sensitivity to the attentional state of a communicative partner by gaze alternating more for an attentive, rather than inattentive, communicative partner.

In the current study, we tested bonobos and chimpanzees because as our closest living relatives they provide the most powerful opportunity for making inferences about our last common ancestor (Hare, 2007; Hare & Yamamoto, 2015). Although equally related to humans, bonobos and chimpanzees have been shown to differ in cognitive development. Bonobos in particular have been observed to show developmental delays relative to chimpanzees in skills relating to foraging, such as spatial navigation (Hare, Wobber, & Wrangham, 2012; Rosati & Hare, 2012; Wobber, Wrangham, & Hare, 2010). These differences may be a result of a selection against aggression in bonobos, because they have less feeding competition than chimpanzees (Hare et al., 2012). A selection against aggression may have promoted extended developmental windows and prolonged juvenile traits that last later in development in bonobos (Hare, 2017). Thus,

these two species may also differ in their development of gaze alternations, suggesting that this skill may have evolved differently between ape species.

2 | METHOD

2.1 | Subjects

Fifty-two semi-free-ranging apes: 17 bonobos (*Pan paniscus*; 7 female, mean age = 7.71 years, range: 3–11) from Lola ya Bonobo Sanctuary in Kinshasa, Democratic Republic of Congo and 35 chimpanzees from Tchimpounga Chimpanzee Sanctuary in Pointe Noire, Republic of Congo (*Pan troglodytes*; 16 female, mean age = 7.48 years, range: 3–11) participated in the study. Twelve additional individuals were tested, but excluded because the mesh enclosure precluded detailed coding of the face (MacLean & Hare, 2015). Primarily, these apes are orphans of the bushmeat or pet trade and arrived at the sanctuary at an early age. They spend the majority of their time with conspecifics in large forested enclosures at the sanctuaries, in species-typical social groups. All apes had regular contact with humans through routine feeding and medical care, and some were raised by human surrogate mothers. A full description of these populations is provided in Wobber and Hare (2011).

2.2 | Procedure and paradigm

Subjects were tested individually in a food-requesting task (Figure 1). The subject was positioned behind a mesh barrier, facing a human experimenter. A video camera was positioned at the subject's eye level to capture a direct recording of eye direction for offline coding. A banana was positioned directly in front of the experimenter, out of the subject's reach. The test consisted of two conditions. In "attentive" trials the experimenter faced the subject, whereas in the "inattentive" trials the experimenter turned his back to the subject (Figure 1). Each trial was 30 seconds long, with four trials per subject; the order of conditions was counterbalanced within subjects in an ABBA design (A = "attentive", B = "inattentive"). At the beginning of the experiment, and again in between each trial, the same experimenter fed the subject bananas for 30 seconds. These feeding breaks were designed to ensure that the subject was interested in obtaining the food and to create a situation in which the subject viewed the experimenter as a potential cooperative partner for obtaining the food.

2.3 | Coding of gaze alternations

Coding was carried out using Datavyu software (www.datavyu.org/). Videos were scored at half-speed. As in previous research with human infants and nonhuman primates, gaze alternations were defined as alternating looks between the experimenter and a target object (i.e., the banana) within a 5-second period¹ (Carpenter et al., 1998; Leavens & Hopkins, 1998; Tomasello et al., 1985). Looks to the food were operationalized as eye saccades and/or head movements in the direction of the food. Looks to the experimenter were operationalized as eye saccades and/or head movements in the direction of the experimenter.

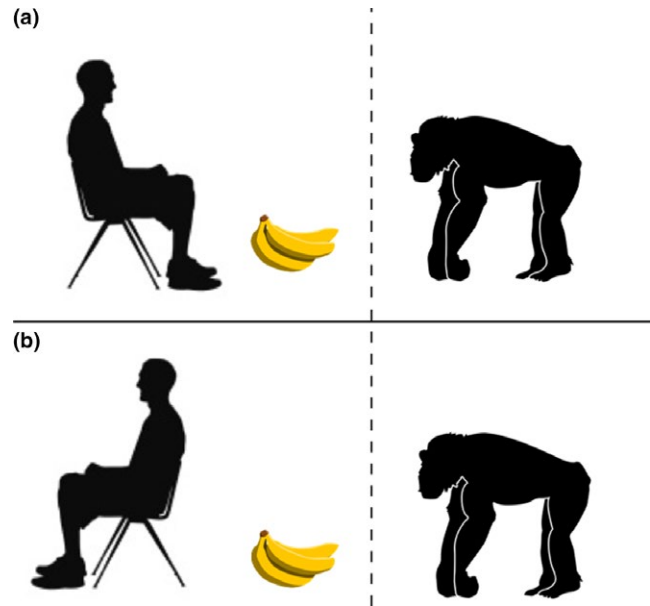


FIGURE 1 Experimental set up for attentive conditions (A) and inattentive conditions (B)

Looks were coded as "away" if the subject did not look at either the food or the experimenter. Twenty percent of all videos were re-coded by an independent coder to establish inter-rater reliability, which was excellent (Cohen's kappa = .81; Landis & Koch, 1977). If the subject looked to the food *and* looked to the experimenter within a 5-second period at least once during a single trial, they were considered to have "gaze alternated" in that trial.

3 | RESULTS

Gaze alternations occurred in 81 of the 208 observed trials. On average, individuals produced gaze alternations in 1.55/4 trials. Over half of the individuals (31/52) produced a gaze alternation in at least one trial. Forty percent of individuals never gaze alternated, 15% gaze alternated in one trial, 13% gaze alternated in two trials, 10% gaze alternated in three trials, and 21% gaze alternated in all four trials.

Linear mixed models (Baayen, Davidson, & Bates, 2008) were used to test whether the number of trials in which individuals produced a gaze alternation varied as a function of the individual's age, species, and experimental condition. Fixed-effect predictors included the individual's age (continuous, in years), species (chimpanzee vs. bonobo), experimental condition (attentive vs. inattentive), sex, and all possible interaction terms. Four repeated observations per individual were taken into consideration by including the individual's ID in the model as a random effect. Likelihood ratio tests (Dobson, 2002) were used to compare the fit of the full model to the null model. Analyses were performed in R (R Development Core Team, 2014) using the function `lmer` of the package `lme4` (Bates & Maechler, 2010). No data points were excluded from analyses because all leverage values (i.e., cook's distance, hat values) were within acceptable limits.

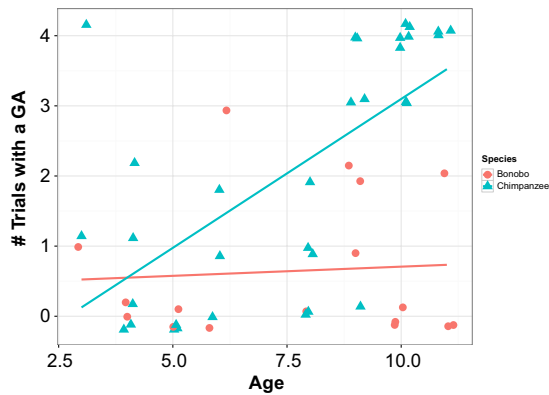


FIGURE 2 Total number of trials with a gaze alternation (GA) based on species and age

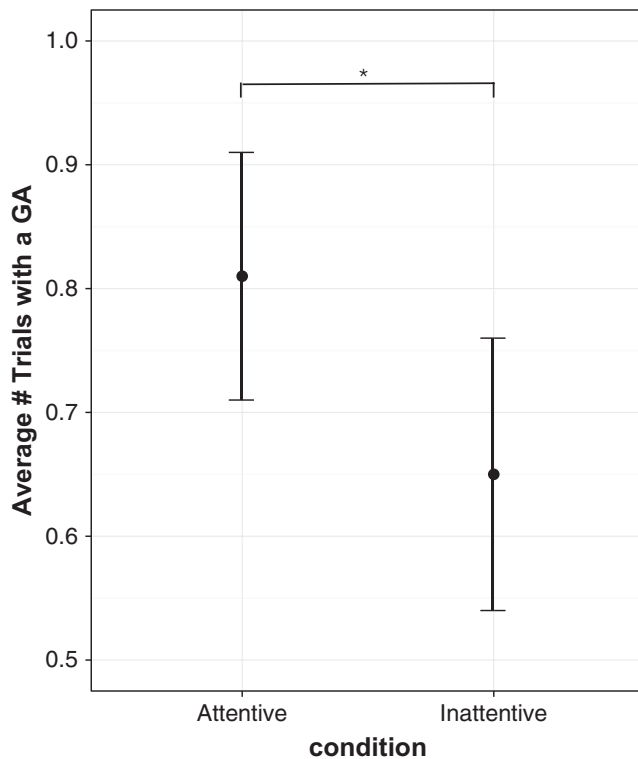


FIGURE 3 Average number of trials (out of two) with gaze alternation (GA) based on experimental condition. Error bars represent standard error of the mean

The only significant interaction to emerge was between age and species ($t = 2.94, p = .005$; Figure 2). There was a significant main effect of condition ($t = 2.02, p = .04$), such that both bonobos and chimpanzees of all ages and both sexes were more likely to gaze alternate during trials in which the experimenter was attentive (average number of trials with a gaze alternation, $M = 0.81, SE = 0.10$), compared to trials in which the experimenter was inattentive ($M = 0.65, SE = 0.11$; Figure 3). There was a marginal effect of sex ($t = 1.76, p = .08$), such that males were slightly more likely to gaze alternate ($M = 0.82, SE = 0.15$) than females ($M = 0.63, SE = 0.15$). Although the sex by species interaction was not significant, there was only one female bonobo, a

juvenile, in the sample of female bonobos ($n = 7$) that gaze alternated. The model including condition and sex as predictors, and the interaction of species and age, fit substantially better than the null model (likelihood ratio test, $\chi^2 = 51.61, df = 5, p < .0001$).

To probe the age by species interaction, the next two analyses tested the effect of age on gaze alternation production within each species (Figure 2). For chimpanzees, age was a significant predictor of gaze alternation production, such that older individuals were significantly more likely to gaze alternate than younger individuals ($t = 4.68, p < .0001$). With each year of life, chimpanzees gaze alternated 5% more often. Alternatively, for bonobos, age was not a significant predictor of gaze alternation production ($p > .05$).

For chimpanzees, there appeared to be a bimodal shift in the effect of age on gaze alternation production, such that individuals only began to increase their gaze alternation production at age 8. To test this, we subset the chimpanzees into two, three-year age groups (younger: 3–6; older: 8–11) and tested for a linear effect of age within each group. For younger chimpanzees, there was no main effect of age on gaze alternation production ($p > .05$). For older chimpanzees, there was a main effect of age on gaze alternation production ($t = 4.42, p = .0001$), such that with each year of life, chimpanzees gaze alternated 12.5% more often. Thus, it appears that age only influences gaze alternation production after the age of 8.

One possible explanation for the main effect of condition (i.e., attentive vs. inattentive trials) is that subjects simply looked more towards the experimenter during attentive trials because they were drawn to the experimenter's face, as opposed to increasing actual gaze alternating behaviors during attentive trials. If this were the case, then subjects' looks towards the experimenter, but not looks towards the food, should increase during attentive trials relative to inattentive trials. A linear mixed model revealed no significant interaction between trial type (attentive vs. inattentive) and behavior type (towards food vs. towards experimenter) on the total number of looks produced ($z = -1.66, p = .10$). In other words, subjects looked more towards both the food and the experimenter during attentive, compared to inattentive trials. Of the 675 times that subjects looked towards the food, 53% of those looks occurred during attentive trials and 47% of those looks occurred during inattentive trials. Of the 184 times subjects looked towards the experimenter, 61% of those looks occurred during attentive trials, and 39% occurred during inattentive trials. There were only main effects of trial type and of behavior type, such that looks towards the food occurred more often than looks toward the experimenter, in both attentive and inattentive trials ($z = 2.73, p = .006$). Additionally, subjects' looks to both the food and the experimenter occurred more often during attentive trials, compared to inattentive trials ($z = 11.32, p < .0001$).

4 | DISCUSSION

We found that similar to human infants, both bonobos and chimpanzees produce gaze alternations with a sensitivity to cues about the attentional state of a communicative partner: they produce more gaze alternations when an experimenter is facing them compared to



when an experimenter is facing away from them. This suggests that bonobos' and chimpanzees' gaze alternations are not simple "checking back" behaviors in which they are checking to see what the other individual is doing, or alternating their gaze between the food and the other individual simply because they are interested in looking at both of them independently. Rather, these findings are consistent with the hypothesis that similar to human infants, bonobos' and chimpanzees' gaze alternations may be used in flexible ways, and be potentially driven by the communicative intent to share attention with others.

Despite their similar ability to gaze alternate with a sensitivity to the attentional state of a communicative partner, we found that the developmental trajectory of bonobos' and chimpanzees' gaze alternations was qualitatively different from humans. Neither bonobos nor chimpanzees produced gaze alternations frequently early in development. This is in contrast to human infants, who produce gaze alternations frequently by 9 months (Mundy et al., 2007). Indeed, a study using a requesting paradigm similar to the one here found that 18-month-olds gaze alternate in 57% of trials (Lucca & Wilbourn, 2016). Chimpanzees increased their production of gaze alternations across ontogeny, but these changes occurred relatively late in development compared to humans, echoing findings on the emergence of gaze following abilities more generally (Carpenter et al., 1998; Tomasello et al., 2001). In contrast, there was no effect of age on the frequency of gaze alternation in bonobos, and bonobos of all ages produced relatively few gaze alternations. Thus, in contrast to humans, who rely on gaze alternations as one of their primary forms of social interaction from the first year of life, gaze alternations appear to be relatively rare in early *Panin* development. This finding builds on a growing body of evidence that humans develop skills related to sharing attention very early on in development (Herrmann, Hare, Call, & Tomasello, 2010; Wobber et al., 2013). The distinctively early emergence of these skills may be what allows for the development of complex social-cognitive abilities, such as language and theory of mind (Tomasello, 2008).

Why might humans, but not bonobos or chimpanzees, produce gaze alternations so frequently from so early on in development? One possibility is that bonobos and chimpanzees may not need to rely on gaze alternations as much as humans. Unlike humans, bonobos and chimpanzees gain control of their hands and are able walk independently of their mother within the first few months of life (Doran, 1997). Thus, bonobos and chimpanzees may not need to rely on communicative skills as heavily as human infants to have their basic needs met. While human infants cannot navigate on their own or gain full control over their hands until later in development, they can control their eye muscles. The human eye is also especially useful for communication because its white sclera is much more salient than other species, making it easier for humans to detect shifts in other humans' eye movements (Kobayashi & Koshima, 1997). One quantitative comparison found that humans' white sclera is three times more visible than that of other great apes (Kaplan & Rogers, 2002). Thus, it is not surprising that human infants, more so than other species, rely on their eyes as a primary means to communicate with others (Tomasello, Hare, Lehmann, & Call, 2007). Future research, directly comparing the frequency of gaze alternations in human infants, bonobos, and

chimpanzees in similar paradigms will allow for more direct and quantitative comparisons of gaze alternations across species.

Although bonobos and chimpanzees did not engage in high rates of gaze alternation, chimpanzees ultimately increased their production of gaze alternations across development whereas bonobos did not. This finding is consistent with prior research suggesting heterochronic changes in the development of certain cognitive skills (e.g., spatial memory) between bonobos and chimpanzees (Hare et al., 2012; Rosati & Hare, 2012; Wobber et al., 2010). These differences likely stem from differences in the feeding ecology and behavior of the two species. In the wild, bonobos have less feeding competition than chimpanzees, which may have led to a selection against aggression in bonobos (Hare et al., 2012; Hohmann & Fruth, 2001; McGrew, 1992; Whiten et al., 1999). This change may have promoted extended developmental windows and prolonged juvenile traits that last later in development in bonobos, explaining why chimpanzees tend to outperform bonobos on various cognitive tasks earlier in life (Hare, 2017; Wobber et al., 2010).

While bonobos have an average life expectancy of 40 years (Rowe, 1996), and typically reach adulthood by 13–14 years, the oldest bonobo in the current sample was 11 years old. If gaze alternations develop on a similar trajectory as other cognitive skills in bonobos, then this sample might be too young to detect an increase in frequency in gaze alternations in bonobos. Indeed, prior research has found that certain social-cognitive skills (e.g., successful social inhibition) only emerge in bonobos older than 10 years (Wobber et al., 2010). Thus, it is possible that with an older sample of bonobos, we would have found that bonobos eventually increased their production of gaze alternations. Alternatively, it may be that bonobos' gaze alternations follow the same developmental trajectory as chimpanzees, but we lacked the ability to detect this trajectory here because we had significantly fewer bonobos ($N = 17$) in our sample than chimpanzees ($N = 35$).

Another limitation of the current study is that we measured gaze alternations during human–ape interactions, rather than mother–infant or conspecific interactions. This is important because studies of animal cognition often find that small changes to a study's design can reveal drastic differences in the underlying abilities those studies are attempting to measure (e.g., Hare, Call, Agnetta, & Tomasello, 2000; Krupenye, Kano, Hirata, Call, & Tomasello, 2016). Although there are some reports that nonhuman apes display heightened social-cognitive skills when interacting with conspecifics compared to humans (Schroepfer-Walker, Wobber, & Hare, 2015), the majority of research in this domain has found no difference in social-cognitive skills of nonhuman apes when interacting with a human compared to conspecific communicative partner (Bräuer, Call, & Tomasello, 2005; Hare & Tomasello, 2004; Itakura, Agnetta, Hare, & Tomasello, 1999). Some studies have even found that chimpanzees have *heightened* social skills in cooperative and communicative tasks when interacting with human experimenters compared to conspecifics (e.g., they are more xenophobic with conspecifics and more xenophilic with humans; Herrmann, Hare, Cissewski, & Tomasello, 2011). Moreover, the apes in the current study have daily experience with humans and many subjects were orphans who were raised with human surrogate mothers beginning in



infancy. This type of lifelong experience with humans may have caused these subjects to become “enculturated” (MacLean, Herrmann, Suchindran, & Hare, 2017; Russell, Lyn, Schaeffer, & Hopkins, 2011), therefore limiting the possibility that they were not motivated to interact or communicate with the human experimenter.

Regardless, future research assessing bonobos' and chimpanzees' gaze alternations with conspecifics will provide additional insights into the nature of bonobos' and chimpanzees' gaze alternations. Another way that future research may shed more light on nonhuman apes' gaze alternations is by utilizing eye-tracking technology to measure gaze alternations. The use of more sophisticated coding technology will allow researchers to capture subtler and more rapid gaze alternations than the human-coded assessments of gaze alteration used here.

In sum, the current findings both replicate prior research by demonstrating that chimpanzees produce gaze alternations, and build on prior work by demonstrating, for the first time, that bonobos also produce gaze alternations. These gaze alternations appeared to be produced in ways that are similar to human infants, and meet a key criterion for goal-directed communication (Bruner, 1981; Tomasello et al., 1994; Woodruff & Premack, 1979). That is, individuals preferentially gaze alternated when a communicative partner was attentive, as opposed to inattentive. This finding suggests that bonobos and chimpanzees took cues of the basic mental state of their communicative partner into account when deciding whether or not to gaze alternate. However, unlike humans, neither bonobos nor chimpanzees produced gaze alternations frequently early in development. Thus, what may be derived in humans is not necessarily the *production* of gaze alternations, but rather the *early* production of gaze alternations. Together with other early-developing social-cognitive skills, the distinctively early emergence of gaze alternations in humans may provide the foundation for the development of complex and important social-cognitive skills, such as language.

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ENDNOTE

¹ In studies of nonhuman animals, operationalizing gaze alternations as alternating looks between a target object and communicative partner that

occur within a multiple-second period, as opposed to in alternating looks in immediate succession, is often used to obtain a more reliable measure of eye movements (e.g., Gaunet & Deputte, 2011; Malavasi & Huber, 2016; Merola, Prato-Previde, & Marshall-Pescini, 2012; Takaoka, Maeda, Hori, & Fujita, 2015).

REFERENCES

- Akhtar, N., & Gernsbacher, M.A. (2007). On privileging the role of gaze in infant social cognition. *Child Development Perspectives*, 2, 59–65.
- Anderson, J.R., Kuwahata, H., & Fujita, K. (2007). Gaze alternation during “pointing” by squirrel monkeys (*Saimiri sciureus*)? *Animal Cognition*, 10, 267–271.
- Baayen, R.H., Davidson, D.J., & Bates, D.M. (2008). Mixed-effects modeling with crossed random effects for subjects and items. *Journal of Memory and Language*, 59, 390–412.
- Bates, D., & Maechler, M. (2010). lme4: Linear mixed-effects models using Eigen and R syntax. R package version 0.999375-35.
- Bates, E., Camaioni, L., & Volterra, V. (1975). The acquisition of performatives prior to speech. *Merrill-Palmer Quarterly of Behavior and Development*, 21, 205–226.
- Bourjade, M., Meguerditchian, A., Maille, A., Gaunet, F., & Vauclair, J. (2014). Olive baboons, *Papio anubis*, adjust their visual and auditory intentional gestures to the visual attention of others. *Animal Behaviour*, 87, 121–128.
- Bräuer, J., Call, J., & Tomasello, M. (2005). All great ape species follow gaze to distant locations and around barriers. *Journal of Comparative Psychology*, 119, 145–154.
- Bruner, J. (1981). Intention in the structure of action and interaction. In L. Lipsitt & C. Rovee-Collier (Eds.), *Advances in infancy research* (1st edn., pp. 129–152). Norwood, NJ: Ablex Publishing.
- Bruner, J.S. (1982). The organisation of action and the nature of adult-infant transaction. In E. Tronick (Ed.), *Social interchange in infancy: Affect, cognition, and communication* (pp. 313–328). Baltimore, MD: University Park Press.
- Bruner, J. (1983). *Child's talk: Learning to use language*. New York: Norton.
- Call, J., & Tomasello, M. (1994). Production and comprehension of referential pointing by orangutans (*Pongo pygmaeus*). *Journal of Comparative Psychology*, 108, 307–317.
- Carpenter, M., Nagell, K., & Tomasello, M. (1998). Social cognition, joint attention, and communicative competence from 9 to 15 months of age. *Monographs of the Society for Research in Child Development*, 63(4, Serial No. 255).
- Desrochers, S., Morissette, P., & Ricard, M. (1995). Two perspectives on pointing in infancy. In C. Moore & P. Dunham (Eds.), *Joint attention: Its origins and role in development* (pp. 85–101). Hillsdale, NJ: Erlbaum.
- Dobson, A. (2002). *An introduction to generalized linear models*. Boca Raton, FL: Chapman and Hall/CRC Press.
- Doran, D.M. (1997). Ontogeny of locomotion in mountain gorillas and chimpanzees. *Journal of Human Evolution*, 32, 323–344.
- Gaunet, F., & Deputte, B.L. (2011). Functionally referential and intentional communication in the domestic dog: Effects of spatial and social contexts. *Animal Cognition*, 14, 849–860.
- Gruber, T., & Zuberbühler, K. (2013). Vocal recruitment for joint travel in wild chimpanzees. *PLoS ONE*, 8, e76073.
- Hare, B. (2007). From nonhuman to human mind: What changed and why? *Current Directions in Psychological Science*, 16, 60–64.
- Hare, B. (2017). Survival of the friendliest: *Homo sapiens* evolved via selection for prosociality. *Annual Review of Psychology*, 68, 155–186.
- Hare, B., Call, J., Agnetta, B., & Tomasello, M. (2000). Chimpanzees know what conspecifics do and do not see. *Animal Behaviour*, 59, 771–785.
- Hare, B., Call, J., & Tomasello, M. (2006). Chimpanzees deceive a human competitor by hiding. *Cognition*, 101, 495–514.
- Hare, B., & Tomasello, M. (2004). Chimpanzees are more skilful in competitive than in cooperative cognitive tasks. *Animal Behaviour*, 68, 571–581.



- Hare, B., Wobber, V., & Wrangham, R. (2012). The self-domestication hypothesis: Evolution of bonobo psychology is due to selection against aggression. *Animal Behaviour*, *83*, 573–585.
- Hare, B., & Yamamoto, S. (2015). Moving bonobos off the scientifically endangered list. *Behaviour*, *152*, 247–258.
- Herrmann, E., Call, J., Hernandez-Lloreda, M.V., Hare, B., & Tomasello, M. (2007). Humans have evolved specialized skills of social cognition: The cultural intelligence hypothesis. *Science*, *317*, 1360–1366.
- Herrmann, E., Hare, B., Call, J., & Tomasello, M. (2010). Differences in the cognitive skills of bonobos and chimpanzees. *PLoS ONE*, *5*, e12438.
- Herrmann, E., Hare, B., Cissewski, J., & Tomasello, M. (2011). A comparison of temperament in nonhuman apes and human infants. *Developmental Science*, *14*, 1393–1405.
- Hohmann, G., & Fruth, B. (2001). Culture in bonobos? Between-species and within-species variation in behavior. *Current Anthropology*, *44*, 563–609. <https://doi.org/10.1086/377649>
- Hostetter, A.B., Hopkins, W.D., & Cantero, M. (2001). Differential use of vocal and gestural communication by chimpanzees (*Pan troglodytes*) in response to the attentional status of a human (*Homo sapiens*). *Journal of Comparative Psychology*, *115*, 337–343.
- Itakura, S., Agnetta, B., Hare, B., & Tomasello, M. (1999). Chimpanzee use of human and conspecific social cues to locate hidden food. *Developmental Science*, *2*, 448–456.
- Kaplan, G., & Rogers, L. (2002). Patterns of gazing in orangutans (*Pongo pygmaeus*). *International Journal of Primatology*, *23*, 501–526.
- Kobayashi, H., & Koshima, S. (1997). Unique morphology of the human eye. *Nature*, *387*, 766–767.
- Krupenye, C., Kano, F., Hirata, S., Call, J., & Tomasello, M. (2016). Great apes anticipate that other individuals will act according to false beliefs. *Science*, *354*, 110–114.
- Landis, J.R., & Koch, G.G. (1977). The measurement of observer agreement for categorical data. *Biometrics*, *33*, 159–174.
- Leavens, D.A., & Hopkins, W.D. (1998). Intentional communication by chimpanzees: A cross-sectional study of the use of referential gestures. *Developmental Psychology*, *34*, 813–822.
- Leavens, D.A., Russell, J.L., & Hopkins, W.D. (2010). Multimodal communication by captive chimpanzees (*Pan troglodytes*). *Animal Cognition*, *13*, 33–40.
- Leung, E.H.L., & Rheingold, H.L. (1981). Development of pointing as a social gesture. *Developmental Psychology*, *17*, 215–220.
- Lucca, K., & Wilbourn, M.P. (2016). Communicating to learn: Infants' pointing gestures result in optimal learning. *Child Development*, <https://doi.org/10.1111/cdev.12707>
- MacLean, E.L. (2016). Unraveling the evolution of uniquely human cognition. *Proceedings of the National Academy of Sciences, USA*, *113*, 201521270.
- MacLean, E.L., & Hare, B. (2012). Bonobos and chimpanzees infer the target of another's attention. *Animal Behaviour*, *83*, 345–353.
- MacLean, E.L., & Hare, B. (2015). Bonobos and chimpanzees exploit helpful but not prohibitive gestures. *Behaviour*, *152*, 493–520.
- MacLean, E.L., Herrmann, E., Suchindran, S., & Hare, B. (2017). Individual differences in cooperative communicative skills are more similar between dogs and humans than chimpanzees. *Animal Behaviour*, *126*, 41–51.
- Malavasi, R., & Huber, L. (2016). Evidence of heterospecific referential communication from domestic horses (*Equus caballus*) to humans. *Animal Cognition*, *19*, 899–909.
- McGrew, W. (1992). *Chimpanzee material culture: Implications for human evolution*. Cambridge: Cambridge University Press.
- Merola, I., Prato-Previde, E., & Marshall-Pescini, S. (2012). Dogs' social referencing towards owners and strangers. *PLoS ONE*, *7*, e47653.
- Mundy, P., Block, J., Delgado, C., Pomares, Y., Van Hecke, A.V., & Parlade, M.V. (2007). Individual differences and the development of joint attention in infancy. *Child Development*, *78*, 938–954.
- Plooij, F.X. (1978). Some basic traits of language in wild chimpanzees? In A.J. Lock (Ed.), *Action, gesture, and symbol: The emergence of language* (pp. 111–131). New York: Academic Press.
- R Development Core Team (2014). *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Rosati, A.G., & Hare, B. (2012). Chimpanzees and bonobos exhibit divergent spatial memory development. *Developmental Science*, *15*, 840–853.
- Rowe, N. (1996). *Pictorial guide to the living primates*. East Hampton, NY: Pogonias Press.
- Russell, J.L., Lyn, H., Schaeffer, J.A., & Hopkins, W.D. (2011). The role of socio-communicative rearing environments in the development of social and physical cognition in apes. *Developmental Science*, *14*, 1459–1470.
- Schroepfer-Walker, K., Wobber, V., & Hare, B. (2015). Experimental evidence that grooming and play are social currency in bonobos and chimpanzees. *Behaviour*, *152*, 545–562.
- Striano, T., & Rochat, P. (2000). Emergence of selective social referencing in infancy. *Infancy*, *1*, 253–264.
- Takaoka, A., Maeda, T., Hori, Y., & Fujita, K. (2015). Do dogs follow behavioral cues from an unreliable human? *Animal Cognition*, *18*, 475–483.
- Tempelmann, S., Kaminski, J., & Liebal, K. (2011). Focus on the essential: All great apes know when others are being attentive. *Animal Cognition*, *14*, 433–439.
- Tomasello, M. (1995). Joint attention as social cognition. In C. Moore & P. Dunham (Eds.), *Joint attention: Its origins and role in development* (pp. 103–130). Hillsdale, NJ: Erlbaum.
- Tomasello, M. (1999). *The cultural origins of human cognition*. Boston, MA: Harvard University Press.
- Tomasello, M., Call, J., Nagell, K., Olguin, R., & Carpenter, M. (1994). The learning and use of gestural signals by young chimpanzees: A trans-generational study. *Primates*, *35*, 137–154.
- Tomasello, M., Carpenter, M., & Liszkowski, U. (2007). A new look at infant pointing. *Child Development*, *78*, 705–722.
- Tomasello, M., George, B., Kruger, A.C., Farrar, M., & Evans, A. (1985). The development of gestural communication in young chimpanzees. *Journal of Human Evolution*, *14*, 175–186.
- Tomasello, M., Hare, B., & Fogleman, T. (2001). The ontogeny of gaze following in chimpanzees, *Pan troglodytes*, and rhesus macaques, *Macaca mulatta*. *Animal Behaviour*, *61*, 335–343.
- Tomasello, M., Hare, B., Lehmann, H., & Call, J. (2007). Reliance on head versus eyes in the gaze following of great apes and human infants: The cooperative eye hypothesis. *Journal of Human Evolution*, *52*, 314–320.
- Whiten, A., Goodall, J., McGrew, W.C., Nishida, T., Reynolds, V., Sugiyama, Y., ... Boesch, C. (1999). Cultures in chimpanzees. *Nature*, *399*, 682–685.
- Wobber, V., & Hare, B. (2011). Psychological health of orphan bonobos and chimpanzees in African sanctuaries. *PLoS ONE*, *6*, e17147.
- Wobber, V., Herrmann, E., Hare, B., Wrangham, R., & Tomasello, M. (2013). Differences in the early cognitive development of children and great apes. *Developmental Psychobiology*, *56*, 547–573.
- Wobber, V., Wrangham, R., & Hare, B. (2010). Bonobos exhibit delayed development of social behavior and cognition relative to chimpanzees. *Current Biology*, *20*, 226–230.
- Woodruff, G., & Premack, D. (1979). Intentional communication in the chimpanzee: The development of deception. *Cognition*, *7*, 333–362.

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