

Research Article

Great Apes' Understanding of Other Individuals' Line of Sight

Sanae Okamoto-Barth,^{1,2} Josep Call,¹ and Michael Tomasello¹¹Department of Developmental and Comparative Psychology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany, and ²Department of Cognitive Neuroscience, Faculty of Psychology, Maastricht University, Maastricht, The Netherlands

ABSTRACT—Previous research has shown that many social animals follow the gaze of other individuals. However, knowledge about how this skill differs between species and whether it shows a relationship with genetic distance from humans is still fragmentary. In the present study of gaze following in great apes, we manipulated the nature of a visual obstruction and the presence/absence of a target. We found that bonobos, chimpanzees, and gorillas followed gaze significantly more often when the obstruction had a window than when it did not, just as human infants do. Additionally, bonobos and chimpanzees looked at the experimenter's side of a windowless obstruction more often than the other species. Moreover, bonobos produced more double looks when the barrier was opaque than when it had a window, indicating an understanding of what other individuals see. The most distant human relatives studied, orangutans, showed few signs of understanding what another individual saw. Instead, they were attracted to the target's location by the target's presence, but not by the experimenter's gaze. Great apes' perspective-taking skills seem to have increased in the evolutionary lineage leading to bonobos, chimpanzees, and humans.

Members of many primate species follow the gaze direction of other individuals to external targets (Tomasello, Call, & Hare, 1998). Interpreting this behavior is not straightforward, however, as it may represent either a simple reflexive tendency to visually orient in the direction of another individual's visual orientation or a more cognitively complex process of knowing that the other "sees" something.

Address correspondence to Sanae Okamoto-Barth, Department of Cognitive Neuroscience, Faculty of Psychology, Maastricht University, P.O. Box 616, 6200 MD Maastricht, The Netherlands, e-mail: s.barth@psychology.unimaas.nl.

Support for the latter interpretation comes from studies in which the looker gazes at a location that, from the point of view of the gaze follower, is behind some obstacle. In this case, if gaze following is due to a co-orientation mechanism, one would expect that the gaze follower would simply look at the barrier or some nearby location. Instead, studies using several different types of barriers have found that individuals of all four species of great ape (humans' closest living relatives)—chimpanzees, bonobos, orangutans, and gorillas—actually move themselves some distance in such a situation so as to gain a good viewing angle on the location to which another individual is looking (whereas they do not do this in several different kinds of control conditions; Bräuer, Call, & Tomasello, 2005; Okamoto, Tanaka, & Tomonaga, 2004; Tomasello, Hare, & Agnetta, 1999). Pre-linguistic human infants, from around 12 months of age, behave in this same way (Moll & Tomasello, 2004).

Following the gaze direction of another individual to a location behind a barrier suggests, at the very least, an attempt to see what is at the location where the other is looking. However, such behavior need not indicate an understanding that the other sees something. Rather, it could be due to a co-orientation mechanism in which the gaze follower attempts to identify the location the looker is fixating (and is motivated to fixate it as well); this mechanism might operate geometrically in space regardless of any obstacles that might initially prevent the gaze follower from zeroing in on the looker's target. Another approach to studying gaze following is therefore to use various kinds of obstacles to block not the gaze follower's visual access to the target, but rather the looker's line of sight to the target. In such cases, the gaze follower is forced to choose among different locations in the looker's line of sight as possible targets of his or her gaze. For example, if a looker's line of sight to an object is blocked by a solid barrier, a gaze follower located on the other side of the barrier might look (erroneously) all the way to the object, might look to the barrier, or, by moving slightly, might look to the looker's side of the barrier. This element of choice makes this

situation a somewhat more demanding test of gaze following and should shed light on its underlying mechanisms.

This blocking-line-of-sight paradigm has been used with human infants around 1 year of age. Specifically, Caron, Kiel, Dayton, and Butler (2002; see also Butler, Caron, & Brooks, 2000; Dunphy-Lelii & Wellman, 2004) had an experimenter sit opposite the infant and look either to the left or right toward a target object on the wall. In one condition, an opaque barrier (a screen) blocked the experimenter's line of sight to the target. In another condition, the screen again was between the experimenter and the target, but the experimenter could see the target clearly through a large window in the screen. Infants as young as 15 months of age looked more often to the target object when the barrier had a window in it than when it did not (12-month-olds did not differentiate in this way).

In the current study, we used the paradigm of Caron et al. (2002) to test the four species of great ape. Subjects witnessed a human experimenter look in the direction of a target object. In one condition, her line of sight was blocked by a solid barrier, whereas in another condition, the barrier had a large window in it so that her line of sight to the object was unimpeded. We predicted that if the apes understood the process of seeing as a psychological process, they would look to the target more when the experimenter was looking through the window than when she was looking at a solid barrier—just as the human infants did in the study by Caron et al. Further, we expected that when the barrier was solid, the apes would in some cases look at the side of the barrier facing the experimenter (a measure not systematically reported for human infants).

We also manipulated a second factor. In the studies of Caron et al., there was always a target object that the infant could see. It is possible that this provided a conflicting cue when the barrier was solid. The gaze follower might have had a prediction or expectation about the presence of a particular object after following the gaze of the looker (Okamoto-Barth & Kawai, 2006). Indeed, in some studies of apes' gaze following in conditions without barriers, when lookers gazed in the direction of an empty location, the apes sometimes “checked back” with the looker (“double looks”), presumably in order to reassess the looker's line of gaze because no target was found (Bräuer et al., 2005; see also Call, Agnetta, & Tomasello, 2000). In the case of human infants, such double looks when no object is seen has been taken as evidence that the gaze follower understands that the looker is not just looking somewhere, but rather is attempting to see something. In the current study, therefore, we used a 2 × 2 design, crossing barrier type (solid vs. window) and (2) target presence (target object present vs. not present).

Including all four great ape species enabled us to assess whether humans' closest living relatives differ in their understanding of seeing in the presence of barriers, and thus to make some inferences about the evolution of this foundational social-cognitive ability. Previous studies have suggested that humans' two closest living relatives, bonobos and chimpanzees, may be

more skillful than gorillas and orangutans in solving a variety of visual perspective-taking problems (e.g., Bräuer et al., 2005; Call & Tomasello, in press; Liebal, Pika, Call, & Tomasello, 2004). These findings suggest that in the evolutionary line leading to humans, the ability to solve such problems may have become especially sophisticated during the last 5 to 6 million years. We predicted that chimpanzees and bonobos would show a greater understanding of the role of barriers in visual perception than would gorillas and orangutans.

METHOD

Subjects

Eight chimpanzees (*Pan troglodytes*), 4 bonobos (*Pan paniscus*), 5 gorillas (*Gorilla gorilla*), and 5 orangutans (*Pongo pygmeus*) participated in this study. All were living in social groups housed in indoor and outdoor areas at the Wolfgang Köhler Primate Research Center at the Leipzig Zoo, Germany. Our sample included 8 males and 14 females from 4 to 33 years old. All subjects had participated in other cognitive studies (see Table 1).

TABLE 1
Age, Sex, and Test History of the Subjects

| Species and name | Gender | Age | Test history ^a |
|-------------------------------------|--------|-----|---------------------------|
| <i>Chimpanzee (Pan troglodytes)</i> | | | |
| Brent | Male | 4 | 1 |
| Patrick | Male | 7 | 1, 2 |
| Robert | Male | 28 | 3 |
| Fifi | Female | 11 | 2, 3 |
| Sandra | Female | 11 | 1, 2, 3 |
| Dorien | Female | 23 | 3 |
| Riet | Female | 26 | 1, 2, 3 |
| Corry | Female | 27 | 3 |
| <i>Bonobo (Pan paniscus)</i> | | | |
| Kuno | Male | 7 | 1, 2, 3 |
| Limbuko | Male | 8 | 1, 2, 3 |
| Joey | Male | 21 | 1, 2, 3 |
| Ulindi | Female | 10 | 1, 2, 3 |
| <i>Gorilla (Gorilla gorilla)</i> | | | |
| N'kwango | Male | 7 | 1 |
| Gorgo | Male | 23 | 1 |
| Ruby | Female | 6 | 1 |
| Bebe | Female | 24 | |
| N'diki | Female | 26 | 1 |
| <i>Orangutan (Pongo pygmeus)</i> | | | |
| Padana | Female | 6 | 1, 2 |
| Toba | Female | 10 | 1, 2 |
| Dokana | Female | 15 | |
| Pini | Female | 16 | 1, 2 |
| Dunja | Female | 33 | 1, 2 |

^aThe numbers in this column indicate the prior studies that included each subject: 1 = Bräuer, Call, and Tomasello (2005); 2 = Barth (2005); 3 = Bräuer, Kaminski, Riedel, Call, and Tomasello (2006). Only in the last two studies were subjects differentially rewarded (e.g., the standard object-choice task); however, they did not perform at above-chance levels.

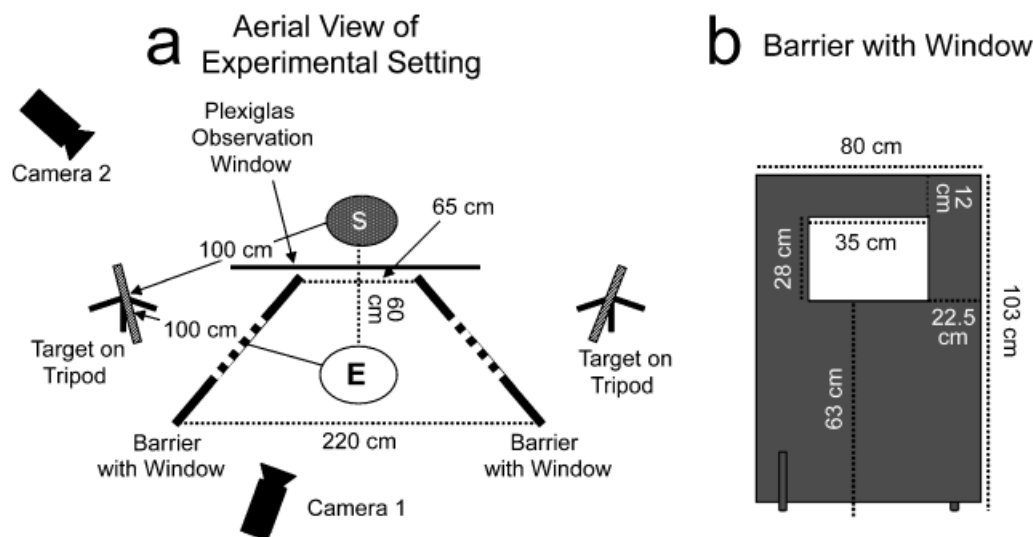


Fig. 1. Aerial view of the experimental setting (a) and illustration of the barrier with a window (b). The locations of the subject and the experimenter are indicated by “S” and “E,” respectively.

Setting

The experiment took place in an indoor testing unit. The experimenter sat facing the subject at a distance of about 60 cm; a Plexiglas observation window separated them (Fig. 1a). The experimenter’s sitting position was adjusted to be at eye level with the subject, and the subject had a clear view of the experimenter throughout the session. On each trial, two identical barriers (opaque barrier or window barrier) were placed on the left and right sides of the experimenter. Each barrier (80 × 103 cm) was a solid, gray plastic board. In the case of the window barriers, a window (28 × 35 cm) was cut in the board at the experimenter’s eye level (Fig. 1b). Two identical tripod stands were used to hold the targets; one was placed approximately 60 cm behind each barrier. On a given trial, identical pictures (e.g., multicolored geometric patterns, animals, landscapes, flowers) were used as targets and fixed on the tripod stands at the subject’s and experimenter’s eye level. The pictures (21 × 30 cm) were changed for each trial to maintain the subject’s interest. They were positioned at an angle visible to both the subject and the experimenter, but only when they turned their heads to see them. The experimenter could actually see the targets only when the barriers had windows.

The experiment was recorded by two digital video cameras. Camera 1 focused on the subjects, and Camera 2 recorded the entire testing area.

Design

There were four conditions resulting from crossing the variables of barrier type and target presence. In the *opaque-barrier/target-present* (*opaque-target*) condition, the opaque barriers were placed at both sides of the experimenter, at right angles to her line of sight to the targets’ locations and clearly blocking

her view. Two identical pictures were used as the targets. The *opaque-barrier/target-absent* (*opaque/no-target*) condition was identical to the *opaque-target* condition except that there were no pictures placed on the tripod stands. The *window-barrier/target-present* (*window-target*) condition was identical to the *opaque-target* condition except that the pair of opaque barriers was replaced by a pair of window barriers. The *window-barrier/target-absent* (*window/no-target*) condition was identical to the *window-target* condition except that there were no pictures placed on the tripod stands.

Procedure

Before each session started, the experimenter stood up behind the barriers and waved at the subject, thus emphasizing the barrier’s opacity or transparency. In the target conditions, the experimenter put the targets on the tripod stands and then went to the experimenter’s central position, whereas in the no-target conditions, she just walked to the tripod-stand areas and then went back to the experimenter’s central position. The order in which target pictures were used was randomized.

At the start of each trial, the experimenter captured the subject’s attention. Once eye contact was established, the experimenter shifted her head and eye orientation toward one of the targets (or the location of a target) for 7 s. A session consisted of 8 trials of the same condition, and different conditions were tested on different days. The four conditions were presented in a counterbalanced block design. Each condition was tested once, for a total of 32 trials.

On all trials, subjects received food rewards. Rewards were given independently of performance to avoid learning effects and to keep subjects motivated to participate in the test and attend to the experimenter.

Data Analysis

We scored three dependent variables from the videotape recordings: looks to the target location, looks at the inside of the barrier (looks at the side of the barrier facing the experimenter), and double looks. All were measured after the experimenter shifted her head and eye orientation to the predetermined location. For each trial, we scored whether or not each kind of look was produced. Double looks were defined as looking at the experimenter again after following the cues to the target location. A second trained coder watched 25% of the video recordings from all subjects and rated the subjects' behavior. The coder could not see the direction in which the experimenter was looking. Agreement between the observers was excellent for all three dependent variables: looks to the target location, 90.8%, $\kappa = .80$; looks at the inside of the barrier, 98.2%, $\kappa = .83$; and double looks, 96.7%, $\kappa = .83$.

Our main analysis consisted of an analysis of variance (ANOVA) on the mean percentage of looks (looks to the target location, looks to inside the barrier, or double looks) with barrier type and target presence as within-subject factors and genus as a between-subjects factor. We conducted Bonferroni-Holm post hoc tests (Holm, 1979) when necessary. Additionally, we used ANOVAs to compare chimpanzees and bonobos directly while excluding the other species. This direct comparison was particularly important because chimpanzees and bonobos are humans' closest living relatives and had a shared ancestor after the split from the ancestor of humans.

Predictions

On the basis of previous research with human and nonhuman primates, we predicted the following four main effects. First, we expected subjects would look to the target location more often in the window conditions than in the opaque conditions. Second, we also expected that subjects would look at the inside of the barrier more often in the opaque conditions than in the window conditions. Third, we predicted that subjects would produce more double looks in the opaque conditions than in the window conditions. Fourth, we predicted that members of the genus *Pan* would show more sensitivity to the gaze of the experimenter in this setup than would gorillas and orangutans. In addition, we assumed that subjects would show differential looking performance depending on the presence or absence of a target; for example, we expected that in the window conditions, subjects would look to the inside of the barrier and would engage in double looks more frequently when the target was absent than when it was present.

RESULTS

Looks at the Target Location

The three genera looked at the target location at comparable levels, $F(2, 19) = 1.15$, $p = .34$, $\eta^2 = .108$, but their looking

behavior varied across the experimental conditions. Subjects looked to the target location more often when there was a window than when the barrier was opaque, $F(1, 19) = 18.02$, $p < .001$, $p_{\text{rep}} = .996$, $\eta^2 = .487$, although a significant Genus \times Barrier Type interaction, $F(2, 19) = 6.33$, $p = .008$, $\eta^2 = .400$, indicated that only chimpanzees and bonobos ($p < .001$) and gorillas ($p = .015$), but not orangutans ($p = .57$), showed this effect.

Additionally, subjects looked at the target location more often in the presence than in the absence of a target, $F(1, 19) = 24.65$, $p < .001$, $p_{\text{rep}} = .999$, $\eta^2 = .565$, but again a significant interaction with genus, $F(2, 19) = 4.06$, $p = .034$, $\eta^2 = .299$, indicated differences among genera. Chimpanzees, bonobos, and gorillas looked to the target location more often in the presence than in the absence of the target, but only when the barrier had a window (*Pan*: $p < .001$, *Gorilla*: $p = .009$), not when the barrier was opaque (*Pan*: $p = .67$, *Gorilla*: $p = .62$). Orangutans also looked at the target location more often when the target object was present than when it was absent, $F(1, 4) = 31.25$, $p = .005$, $p_{\text{rep}} = .982$, $\eta^2 = .887$, but unlike subjects of the other genera, they did so regardless of the barrier, $F(1, 4) = 0.21$, $p = .68$, $p_{\text{rep}} = .611$, $\eta^2 = .049$.

A direct comparison between chimpanzees and bonobos showed a significant Object Presence \times Species interaction, $F(1, 10) = 5.03$, $p = .049$, $p_{\text{rep}} = .921$, $\eta^2 = .334$; in the presence of a target, bonobos looked at the target location more often than did chimpanzees.

Looks at the Inside of the Barrier

The three genera differed in the percentage of trials with looks directed at the inside of the barrier, $F(2, 19) = 6.40$, $p = .007$, $\eta^2 = .403$. Post hoc tests indicated that orangutans looked at the inside of the barrier significantly less often than did chimpanzees and bonobos ($p = .004$) and gorillas ($p = .005$). Moreover, a significant Barrier Type \times Genus interaction, $F(2, 19) = 7.56$, $p = .004$, $\eta^2 = .443$, indicated that chimpanzees and bonobos looked at the inside of the barrier more often when it was opaque than when it had a window ($p = .028$), whereas gorillas looked at the inside of the barrier more often when it had a window than when it was opaque ($p = .016$). Interestingly, bonobos did not look at the inside of the barrier in the window condition.

A direct comparison between chimpanzees and bonobos revealed a significant Barrier Type \times Object Presence \times Species interaction, $F(1, 10) = 10.76$, $p = .008$, $p_{\text{rep}} = .973$, $\eta^2 = .518$. Bonobos and chimpanzees differed in how presence versus absence of the target influenced looking at the inside of the barrier in the opaque condition. Whereas bonobos looked at the inside of the barrier more when a target was present, chimpanzees looked at the barrier more when the target was absent.

Double Looks

The three genera differed in the percentage of double looks that they produced, $F(2, 19) = 4.07$, $p = .034$, $\eta^2 = .300$. Post hoc

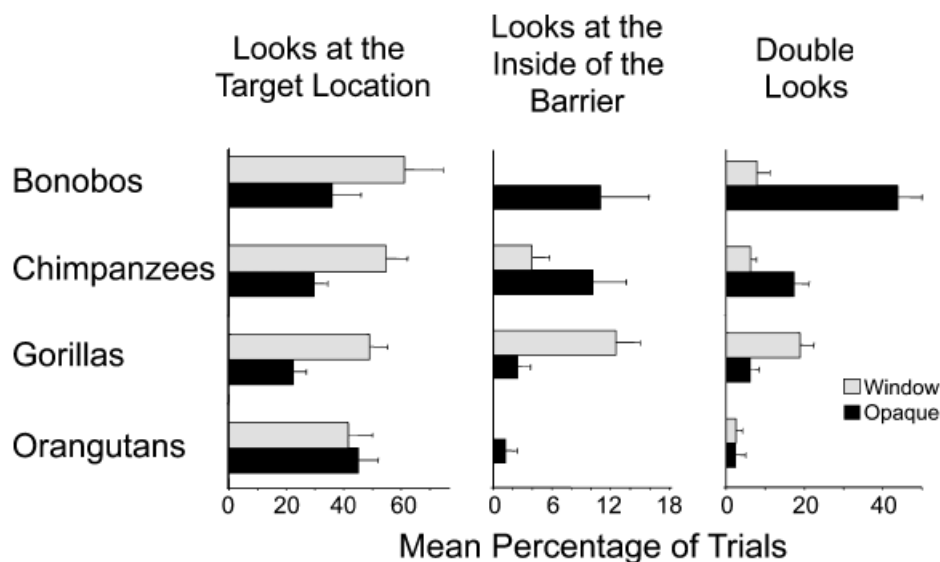


Fig. 2. Percentage of trials with looks at the target location, looks at the inside of the barrier, and double looks as a function of barrier type and species. The percentages shown are averages across the target and no-target conditions.

tests indicated that members of the genus *Pan* made significantly more double looks than did orangutans ($p = .01$). Moreover, the three genera differed in the distribution of double looks across conditions, as indicated by a significant Genus \times Barrier Type interaction, $F(2, 19) = 7.56, p = .004, \eta^2 = .443$. Chimpanzees and bonobos produced more double looks when the barrier was opaque than when it had a window ($p = .004$), whereas gorillas ($p = .15$) and orangutans ($p = 1.0$) were unaffected by barrier type. Additionally, an interaction between barrier type and target presence, $F(1, 19) = 5.06, p = .037, p_{rep} = .934, \eta^2 = .210$, indicated that in the window-barrier conditions, subjects produced more double looks when the target was absent than when it was present, whereas the opposite was true in the opaque-barrier conditions.

Bonobos produced more double looks than chimpanzees, $F(1, 10) = 6.90, p = .025, p_{rep} = .947, \eta^2 = .408$, although a significant Barrier Type \times Species interaction, $F(1, 10) = 8.49, p = .015, p_{rep} = .962, \eta^2 = .459$, indicated that this effect was especially marked when the barrier was opaque.

Summary

Figure 2 summarizes the findings for the three measures as a function of barrier type and species. Chimpanzees, bonobos, and gorillas looked at the target location more in the window conditions than in the opaque conditions (but only when a target was present). For this measure, orangutans showed no effect of barrier type (and they looked at the target location more when a target was present than when there was no target). Chimpanzees and bonobos looked at the inside of the barrier more often when it was opaque than when it had a window, whereas gorillas looked at the inside of the barrier more often when it had a

window. Orangutans rarely looked at the inside of the barrier, regardless of condition. Finally, chimpanzees and especially bonobos produced more double looks in the opaque conditions than in the window conditions. Gorillas showed the opposite pattern, producing more double looks in the window condition. Orangutans produced few double looks and their frequency of double looks was unaffected by the barrier type (or by the presence of a target).

DISCUSSION

Using a visual obstruction paradigm previously used with human infants, we investigated whether great apes understand the referential nature of looking. Chimpanzees and bonobos responded like human infants in similar situations (Caron et al., 2002). They followed gaze more often when the experimenter looked through a barrier with a window rather than at a barrier without a window, and they looked more often at the inside of the barrier and produced more double looks when the barrier lacked a window than when it had a window. Additionally, bonobos produced more double looks when the barrier was opaque than when it had a window. These results, combined with others showing that these species also follow gaze around barriers (Bräuer et al., 2005; Povinelli & Eddy, 1996; Tomasello et al., 1999), produce double looks when they cannot detect a target (Bräuer et al., 2005; Call, Hare, & Tomasello, 1998), and are sensitive to the gaze of the experimenter (although not as much as human infants; Tomasello, Hare, Lehmann, & Call, in press), suggest that chimpanzees and bonobos have some understanding of the referential nature of looking.

Although gorillas, like human infants, also looked more at the target location when the barrier had a window than when

it was opaque, they did not inspect the inside of the barrier or engage in double looks when confronted with a windowless barrier. In fact, they inspected the inside of the barrier more often when it had a window. Orangutans were even less sensitive than gorillas to this barrier feature, not even following gaze differentially depending on the presence of the window. It is conceivable that orangutans, which followed the experimenter's gaze at levels comparable to the levels of the other species, possess no clear understanding of the referential nature of looking. Instead, they may have simply been attracted to the target location by the target's presence. Thus, these results confirm previous studies showing that chimpanzees and bonobos were more sensitive than gorillas and orangutans in visual perspective-taking tasks.

Our results could be explained as an artifact due to using a human to give gaze cues. Thus, it may not be the case that chimpanzees and bonobos are more cognitively sophisticated than other species in this task; they might simply attend more to humans. However, some studies have detected differences between chimpanzees and bonobos, on the one hand, and gorillas and orangutans, on the other, without the participation of humans. For instance, chimpanzees and bonobos show greater sensitivity than the other apes in adjusting gesture modality (visual vs. tactile) to the attentional state of the recipient (Call & Tomasello, in press). Chimpanzees also show social contagion; that is, they increase yawning after watching movies of conspecifics yawning (Anderson, Myowa-Yamakoshi, & Matsuzawa, 2004). Anderson et al. (2004) have suggested that this social contagion may be related to some form of empathic responses. Arguably, greater attention to other individuals in general, not just to humans, among chimpanzees and bonobos could still explain our results. However, under this hypothesis, it is unclear why all four species followed gaze at comparable levels, differing only in how they deployed their attention to various locations. Thus, our working hypothesis is that bonobos and chimpanzees, who live in the most complex ape societies (with fission-fusion organization), may have evolved more sophisticated social-cognitive skills of perspective taking than the other great apes.

Despite the overall similarity in results for chimpanzees and bonobos, these species differed from each other in some respects. Bonobos looked at the target location more often than chimpanzees in the presence of a target object in the window condition. This suggests that compared with chimpanzees, bonobos might inhibit more of their gaze-following responses when there is no target object. Additionally, although both chimpanzees and bonobos produced more double looks in the opaque conditions than the window conditions, bonobos produced more double looks than chimpanzees. Interestingly, whereas bonobos looked at the inside of the barrier more when a target was present, chimpanzees looked at the inside of the barrier more when the target was absent. These results again suggest that bonobos may understand the referential nature of looking better than chimpanzees.

Currently, it is unclear whether any other species understand the referential nature of looking to the same extent that chimpanzees and bonobos do. Many species follow the gaze of conspecifics or humans to distal targets (monkeys: Anderson & Mitchell, 1999; Emery, Lorincz, Perrett, Oram, & Baker, 1997; Tomasello et al., 1998; dolphins: Tschudin, Call, Dunbar, Harris, & van der Elst, 2001; ravens: Bugnyar, Stowe, & Heinrich, 2004; dogs: Hare, Call, & Tomasello, 1998; Miklósi, Polgárdi, Topál, & Csányi, 1998; goats: Kaminski, Riedel, Call, & Tomasello, 2005). In addition, ravens follow gaze around barriers (Bugnyar et al., 2004), Diana monkeys produce double looks (Scerif, Gómez, & Byrne, 2004), and pigtail macaques can use eye direction, not just head direction, to locate targets (Ferrari, Kohler, Fogassi, & Gallese, 2000). Although these are intriguing findings, perhaps suggesting that animals besides chimpanzees and bonobos have some grasp of referentiality, the data are still too fragmentary. Additional studies are needed to reach solid conclusions.

In conclusion, chimpanzees and bonobos, like 15-month-old human infants, responded to the obstruction of a human's line of sight in a way that suggests they understood the referential nature of looking. Gorillas also followed the gaze of the experimenter more often in the presence of barriers with windows than in the presence of opaque barriers. However, other indicators (looking at the inside of the barrier and double looks) suggested that gorillas' knowledge in this domain may not be as robust as that of their cousins. In contrast, this study provided little evidence that orangutans are sensitive to the referential nature of looking. The resulting ordering of these species in terms of their increasing sophistication in this task (orangutans, gorillas, chimpanzees, and bonobos) fits well with their genetic distance from humans. Thus, perspective-taking skills, including understanding of the referential nature of gaze direction, may have gradually increased in the evolutionary lineage leading to bonobos, chimpanzees, and humans.

Acknowledgments—We thank the keepers of the Wolfgang Köhler Primate Research Center for their assistance with the experiment. We also thank two anonymous reviewers and Jochen Barth for helpful comments on the manuscript.

REFERENCES

- Anderson, J.R., & Mitchell, R.W. (1999). Macaques but not lemurs co-orient visually with humans. *Folia Primatologica*, 70, 17–22.
- Anderson, J.R., Myowa-Yamakoshi, M., & Matsuzawa, T. (2004). Contagious yawning in chimpanzees. *Proceedings of the Royal Society B*, 271, S468–S470.
- Barth, J. (2005). *Search and exploration of hidden objects by great apes and young children*. Maastricht, The Netherlands: Universitaire Pers Maastricht.
- Bräuer, J., Call, J., & Tomasello, M. (2005). All four great ape species follow gaze around barriers. *Journal of Comparative Psychology*, 119, 145–154.

- Bräuer, J., Kaminski, J., Riedel, J., Call, J., & Tomasello, M. (2006). Making inferences about the location of hidden food: Social dog, causal ape. *Journal of Comparative Psychology*, *120*, 38–47.
- Bugnyar, T., Stowe, M., & Heinrich, B. (2004). Ravens, *Corvus corax*, follow gaze direction of humans around obstacles. *Proceedings of the Royal Society B*, *271*, 1331–1336.
- Butler, S.C., Caron, A.J., & Brooks, R. (2000). Infant understanding of the referential nature of looking. *Journal of Cognition and Development*, *1*, 359–377.
- Call, J., Agnetta, B., & Tomasello, M. (2000). Social cues that chimpanzees do and do not use to find hidden objects. *Animal Cognition*, *3*, 23–34.
- Call, J., Hare, B., & Tomasello, M. (1998). Chimpanzee gaze following in an object choice task. *Animal Cognition*, *1*, 89–100.
- Call, J., & Tomasello, M. (in press). Comparing the gestural repertoires of apes. In J. Call & M. Tomasello (Eds.), *The gestural communication of apes and monkeys*. New York: Erlbaum.
- Caron, A.J., Kiel, E.J., Dayton, M., & Butler, S.C. (2002). Comprehension of the referential intent of looking and pointing between 12 and 15 months. *Journal of Cognition and Development*, *3*, 445–464.
- Dunphy-Lelii, S., & Wellman, H.M. (2004). Infants' understanding of occlusion of others' line-of-sight: Implications for an emerging theory of mind. *European Journal of Developmental Psychology*, *1*, 49–66.
- Emery, N.J., Lorincz, E.N., Perrett, D.I., Oram, M.W., & Baker, C.I. (1997). Gaze following and joint attention in rhesus monkeys (*Macaca mulatta*). *Journal of Comparative Psychology*, *111*, 286–293.
- Ferrari, P.F., Kohler, E., Fogassi, L., & Gallese, V. (2000). The ability to follow eye gaze and its emergence during development in macaque monkeys. *Proceedings of the National Academy of Sciences, USA*, *97*, 13997–14002.
- Hare, B.H., Call, J., & Tomasello, M. (1998). Communication of food location between human and dog (*Canis familiaris*). *Evolution of Communication*, *2*, 137–159.
- Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, *6*, 65–70.
- Kaminski, J., Riedel, J., Call, J., & Tomasello, M. (2005). Domestic goats (*Capra hircus*) follow gaze direction and use social cues in an object choice task. *Animal Behaviour*, *69*, 11–18.
- Liebal, K., Pika, S., Call, J., & Tomasello, M. (2004). To move or not to move: How apes alter the attentional states of humans when begging for food. *Interaction Studies*, *5*, 199–219.
- Miklósi, A., Polgárdi, R., Topál, J., & Csányi, V. (1998). Use of experimenter-given cues in dogs. *Animal Cognition*, *1*, 113–121.
- Moll, H., & Tomasello, M. (2004). 12- and 18-month-olds follow gaze behind barriers. *Developmental Science*, *7*, F1–F9.
- Okamoto, S., Tanaka, M., & Tomonaga, M. (2004). Looking back: The “representational mechanism” of joint attention in an infant chimpanzee (*Pan troglodytes*). *Japanese Psychological Research*, *46*, 236–245.
- Okamoto-Barth, S., & Kawai, N. (2006). The role of attention in the facilitation effect and another “inhibition of return.” *Cognition*, *101*, B42–B50.
- Povinelli, D.J., & Eddy, T.J. (1996). Chimpanzees: Joint visual attention. *Psychological Science*, *7*, 129–135.
- Scerif, G., Gómez, J.C., & Byrne, R.W. (2004). What do Diana monkeys know about the focus of attention of a conspecific? *Animal Behaviour*, *68*, 1239–1247.
- Tomasello, M., Call, J., & Hare, B. (1998). Five primate species follow the visual gaze of conspecifics. *Animal Behaviour*, *55*, 1063–1069.
- Tomasello, M., Hare, B., & Agnetta, B. (1999). Chimpanzees, *Pan troglodytes*, follow gaze direction geometrically. *Animal Behaviour*, *58*, 769–777.
- Tomasello, M., Hare, B., Lehmann, H., & Call, J. (in press). Reliance on head versus eyes in the gaze following of great apes and human infants: The cooperative eye hypothesis. *Journal of Human Evolution*.
- Tschudin, A., Call, J., Dunbar, R.I.M., Harris, G., & van der Elst, C. (2001). Comprehension of signs by dolphins (*Tursiops truncatus*). *Journal of Comparative Psychology*, *115*, 100–105.

(RECEIVED 5/1/06; REVISION ACCEPTED 7/11/06;
FINAL MATERIALS RECEIVED 7/17/06)