

All Great Ape Species Follow Gaze to Distant Locations and Around Barriers

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Following the gaze direction of conspecifics is an adaptive skill that enables individuals to obtain useful information about the location of food, predators, and group mates. In the current study, the authors compared the gaze-following skills of all 4 great ape species. In the 1st experiment, a human either looked to the ceiling or looked straight ahead. Individuals from all species reliably followed the human's gaze direction and sometimes even checked back when they found no target. In a 2nd experiment, the human looked behind some kind of barrier. Results showed that individuals from all species reliably put themselves in places from which they could see what the experimenter was looking at behind the barrier. These results support the hypothesis that great apes do not just orient to a target that another is oriented to, but they actually attempt to take the visual perspective of the other.

Keywords: gaze-following, social cognition, joint attention

Following the gaze of other individuals is an adaptive skill that enables individuals to obtain useful information about the location of food, predators, and group mates. There is strong evidence that nonhuman primates and other animals have this skill (Emery, Lorincz, Perrett, & Oram, 1997; Kaminski, Riedel, Call, & Tomasello, 2005; Miklosi, Polgardi, Topal, & Csanyi, 1998; Tomasello, Call, & Hare, 1998). For instance, Tomasello et al. (1998) tested gaze following using conspecifics in five primate species (*Pan troglodytes*, *Cercocebus atys torquatus*, *Macaca mulatta*, *M. arcoides*, and *M. nemestrina*). With two individuals facing each other, one of them was induced to look at food being displayed from an observation tower. Once this subject was looking up to the food, the authors measured whether the other individual, on seeing its partner look up, turned around and also looked up toward the food location. Tomasello et al. (1998) found that individuals from all five species reliably followed the gaze of conspecifics. Additional studies have shown that chimpanzees also follow the visual gaze direction of humans—even when the target is above and behind them (Itakura, 1996) or when the human just moves her eyes without any movement of the head (Povinelli & Eddy, 1996).

Two models have been proposed to explain the cognitive mechanisms underlying gaze-following behavior. The orienting-response model postulates that animals have a tendency to look in the direction that others are looking. Individuals have learned that the gaze direction of others is a useful cue for detecting something interesting. So, one can follow gaze using this simple rule: if the eyes (or head) of the partner turn to the left then look at the left side, whereas if they go to the right then look at the right side (Emery, 2000). Note that this model makes no prediction about the

reason for looking, it is just about orientation. The perspective-taking model, like the orienting-response model, postulates that gaze following is based on an orienting response, but it also postulates that the observer understands that when others look in a certain direction it is because they are seeing something interesting or unusual. In other words, the perspective-taking model, unlike the orienting-response model, postulates content to the gaze-following response. Note that learning can be involved for both mechanisms. Animals can learn that the gaze direction of others is a useful cue for detecting something interesting (orienting-response model), or they can develop their understanding of the meaning of the gaze—that others see something different from themselves (perspective-taking model).

There are three lines of evidence that chimpanzees do not just respond automatically to the gaze of humans or conspecifics, thus casting some doubt on the validity of the orienting-response model. First, Call, Hare, and Tomasello (1998) found in their study that when a chimpanzee tracked the gaze of a human to a location and found nothing interesting there, they quite often looked back to the individual's face and tracked their gaze direction a second time (the so-called *double looks*). This phenomenon has also been described in human infants (e.g., Butterworth & Cochran, 1980; Scaife & Bruner, 1975) and can be interpreted as evidence that subjects understood that gaze was about something specific in the environment (i.e., it has content). However, Call et al. (1998) pointed out that it was also possible that subjects simply returned to their normal visual orientation after finding nothing of interest and that the second look to the ceiling was just a second automatic response to the human's head orientation (Call et al., 1998; see also Moore & Corkum, 1998, for alternative interpretations).

Second, following a suggestive finding of Povinelli and Eddy (1996), Tomasello, Hare, and Agnetta (1999) found that chimpanzees follow the gaze direction of other animate beings geometrically to specific locations in much the same way as humans. They conducted two experiments. In the first experiment, chimpanzees watched as a human experimenter looked around various types of

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barriers. The subjects looked around each of the barriers more often when the human had done so than in a control condition in which the human looked in another direction. In the second experiment, chimpanzees watched as a human looked toward the back of their cage. As they turned to follow the human's gaze, a distracter object was presented. The chimpanzees looked at the distracter while still following the human's gaze to the back of the cage. The authors argued that these results effectively disconfirmed the orienting-response model of chimpanzee gaze following (Tomasello et al., 1999).

Third, there is data showing that there is a developmental progression in gaze-following response. Macaques and chimpanzee infants do not respond reliably before the age of 5–6 and 36–48 months, respectively (Tomasello, Hare, & Fogelman, 2001). Although Okamoto et al. (2002) also found a developmental change, the age of emergence in their subject was much earlier—they detected reliable gaze-following responses to head orientation and eye orientation alone at the age of 11 and 13 months, respectively. Okamoto et al. (2002) pointed out that a possible explanation for this discrepancy between studies was that, in their study, the experimenter always looked at a target that was in the subject's view, whereas the experimenter in the Tomasello et al. (2001) study always looked into empty space outside the visual field of the subject. Human infants also gaze follow more readily if the target is within their visual field (Butterworth & Jarrett, 1991). Tomasello et al. (2001) also found another interesting developmental piece of evidence. On observing a human experimenter repeatedly looking up into empty space, adult chimpanzees, but not infant chimpanzees, habituated and stopped responding. This may suggest that adults can overwrite the orienting response because they know that there is actually nothing unusual to look at, whereas infants are more tightly controlled by the orienting response.

Compared with the information available on chimpanzee gaze following, little is known about the gaze-following abilities of the other three great ape species. Schaller noted that direct stare in gorillas (*Gorilla gorilla*) was a form of threat both against conspecifics and also against humans (Schaller, 1963). Peignot and Anderson (1999) reported that gorillas tested in an object-choice paradigm avoided looking into the eyes of a human experimenter, and looking into the eyes of others would seem to be a prerequisite to follow gaze. However, it is also true that staring among gorillas was observed in various social contexts (Yamagiwa, 1992). In a study about patterns of gazing in orangutans (*Pongo pygmaeus*), Kaplan and Rogers (2002) discovered that these animals also avoid direct staring. It is interesting that they only detected two incidences of gaze following out of more than 200 gaze episodes toward conspecifics. Because orangutans live a semisolitary existence (Delgado & van Schaik, 2000), one might expect that visual communication does not play such a big role as for the other great ape species. A similar lack of information exists for bonobos (*Pan paniscus*). Although the close genetic relation between bonobos and chimpanzees (Bradley & Vigilant, 2002) may suggest similar abilities in gaze-following behavior, it is also true that these two species show marked differences in many social behaviors (see Boesch, Hohmann, & Marchant, 2002 and Stanford, 1998 for a debate on this issue). Therefore, it is uncertain how similar bonobos will be to chimpanzees in gaze-following behavior.

The current study had two aims. First, we wanted to compare the gaze-following skills of chimpanzees with those of bonobos, gorillas, and orangutans, for whom little systematic information exists. Second, we wanted to further investigate the possible cognitive mechanisms underlying gaze-following behavior in chimpanzees and other great apes. Thus, we tested the predictions of the orienting-response and perspective-taking models in two different experiments. The first experiment used the Call et al. (1998) procedure in which a human experimenter looked at the ceiling right above the subjects' position, whereas, in the control condition, the experimenter looked at the subject. This experiment assessed the basic gaze-following response across species and whether, on looking up and seeing nothing unusual, individuals would produce double looks. The second experiment used the Tomasello et al. (1999) procedure in which the experimenter looked around various types of barriers. This experiment tested whether the great apes really track the visual gaze of humans to specific targets.

The combination of these two experiments allowed us to contrast the predictions derived from the orienting-response and perspective-taking models. If gaze-following behavior is solely based on an orientation response, we would expect that (a) after gaze following and seeing nothing, subjects should not perform double looks because they have already performed the orienting response, and (b) after gaze following and seeing an opaque barrier, subjects should not move to look around the barrier, because they have already performed the orienting response and detected an object (the barrier). Moreover, the presence of clear developmental changes in these skills would lend additional support to the perspective-taking model as it suggests a role for cognitive factors.

Experiment 1: Gaze Following to a Location Above the Subject

Method

Subjects. We tested 6 orangutans (*Pongo pygmaeus*), 6 gorillas (*Gorilla gorilla*), 4 bonobos (*Pan paniscus*), and 11 chimpanzees (*Pan troglodytes*) of various ages (range: 2.5–30.0 years olds; see Table 1). All subjects lived in groups with their conspecifics in the Wolfgang Köhler Primate Center in the Leipzig Zoo (Germany). They were housed in enclosures with outdoor and indoor areas and sleeping cages for the night. The subjects were all born in captivity except for two gorillas who were wild born. Although the nursery-raised individuals were reared by humans early in ontogeny, they mostly grew up with peers from a fairly early age and did not receive any special treatment leading to human enculturation (Annett and Alexandra had more extensive contact with humans only after this experiment). All other subjects were raised normally by their mothers. Subjects were all tested by the same female experimenter, whom they came to know some weeks before the experiment.

Materials. Testing took place in special testing rooms (25 m²). They were divided by wire mesh and Plexiglas into two parts, so that the ape was on one side and the experimenter sat on the other side. Pieces of bananas, grapes, and apples were used to feed the apes between the trials. The whole experiment was videotaped from behind the experimenter.

Procedure. Each subject was tested individually. In most cases, it was possible that the apes stayed alone in their cage. In those cases in which another ape was present (because subjects were reluctant to be alone), the trial was only started when the tested ape did not interact with the conspecific. We followed the procedure used by Call et al. (1998). The

Table 1
Subjects That Participated in Experiments 1 and 2

Subject	Species	Gender	Age and group	Rearing history	Experiment
Fraukje	Chimpanzee	Female	25 (adult)	Nursery/peers	1, 2
Riet	Chimpanzee	Female	24 (adult)	Nursery/peers	1, 2
Ulla	Chimpanzee	Female	24 (adult)	Nursery/peers	1, 2
Natascha	Chimpanzee	Female	21 (adult)	Nursery/peers	1, 2
Sandra	Chimpanzee	Female	8 (juvenile)	Neutered	1, 2
Frodo	Chimpanzee	Male	8 (juvenile)	Mother	1, 2
Patrick	Chimpanzee	Male	4 (infant)	Mother	1
Brent	Chimpanzee	Male	2.5 (infant)	Mother	1
Pia	Chimpanzee	Female	2.5 (infant)	Mother	1
Annette	Chimpanzee	Female	2.5 (infant)	Nursery/peers	1
Alexandra	Chimpanzee	Female	2.5 (infant)	Nursery/peers	1
Joey	Bonobo	Male	19 (adult)	Nursery/peers	1, 2
Ulindi	Bonobo	Female	8 (juvenile)	Mother	1, 2
Limbuko	Bonobo	Male	6 (juvenile)	Nursery/peers	1, 2
Kuno	Bonobo	Male	5 (juvenile)	Nursery/peers	1, 2
Bebe	Gorilla	Female	22 (adult)	Wildborn	1, 2
Gorgo	Gorilla	Male	20 (adult)	Nursery/peers	1, 2
Vimoto	Gorilla	Male	6 (juvenile)	Mother	1
Vizuri	Gorilla	Female	6 (juvenile)	Mother	1
Viringika	Gorilla	Female	6 (juvenile)	Mother	1, 2
Ruby	Gorilla	Female	4 (infant)	Mother	1, 2
Ndiki	Gorilla	Female	26 (adult)	Wildborn	2
Kwango	Gorilla	Male	7 (juvenile)	Mother	2
Dunja	Orangutan	Female	30 (adult)	Mother	1, 2
Bimbo	Orangutan	Male	21 (adult)	Mother	1, 2
Pini	Orangutan	Female	13 (adult)	Mother	1, 2
Walter	Orangutan	Male	12 (adult)	Nursery/peers	1, 2
Toba	Orangutan	Female	7 (juvenile)	Mother	1, 2
Padana	Orangutan	Female	3.5 (infant)	Mother	1, 2

Note. See *Subjects* paragraph under Experiment 1 for explanation of rearing history terms.

experimenter sat in front of the ape. She fed the subject a predetermined number of food pieces (1–4 pieces, one after another). Then, she took the next piece of food and held it in her hand in front of the ape. In that moment, a trial started. The experimenter behaved differently depending on the two experimental conditions:

Gaze-at-ceiling: The experimenter suddenly raised her head and looked at the ceiling to a location right above the ape. This was the experimental condition.

Gaze-at-subject: The experimenter looked at the subject. This was the control condition.

Each trial lasted 10 s. After that, the experimenter gave the piece of food to the subject. This was completely independent from what the ape had done during the trial.

We gave each subject six experimental trials and six control trials. The presentation of experimental and control trials alternated throughout a session. Half of the subjects started with an experimental trial, and the other half started with a control trial. A session usually consisted of six trials (three experimental and three control trials), meaning that most of the animals were tested for 2 days. If after some trials an ape did not stay close to the experimenter to get the food, which happened with some infants, the session was stopped and continued the next day.

Scoring. All trials were scored from the videotapes. We scored both initial looks and double looks. First, a coder who was unaware of the condition that the ape had received coded whether the ape looked up or not in a given trial. Second, another observer coded whether the subject performed a double look during the trial. We defined a double look as looking up, looking at the experimenter, and looking up again within the

trial. To analyze the potential effects on gaze following of variables such as species, sex, or age (infant = 1–4 years, juvenile = 5–10 years, adult = 10+ years), we used the difference between the experimental and control conditions for each subject. A positive score would mean that subjects looked more often in the experimental than in the control condition, whereas a negative score would indicate that subjects looked up more in the control compared with the experimental condition. A second independent observer scored 20% of the trials to assess interobserver reliability. Interobserver reliability was good (Cohen's $\kappa = 0.73$, $N = 70$). We used nonparametric statistics because the homogeneity of variance assumption was violated. All tests were two-tailed except those involving age comparisons for the initial looks, as previous studies had shown that adults were more likely than infants to produce gaze-following responses.

Results

Initial looks. Overall, subjects looked up significantly more often in the gaze-at-ceiling condition compared with the gaze-at-subject (control) condition, Wilcoxon's $T(N = 23) = 264$, $p < .001$. Figure 1 presents the looking frequency across conditions for each species. There were no significant effects on the difference between gaze following in the experimental and control conditions for species, Kruskal–Wallis $\chi^2(3) = 4.73$, $p = .19$, or sex, Kruskal–Wallis $\chi^2(1) = 0.51$, $p = .48$. Although chimpanzees and bonobos showed the highest response rate in the experimental condition, there were no statistical differences across species, Kruskal–Wallis $\chi^2(3) = 3.02$, $p = .39$.

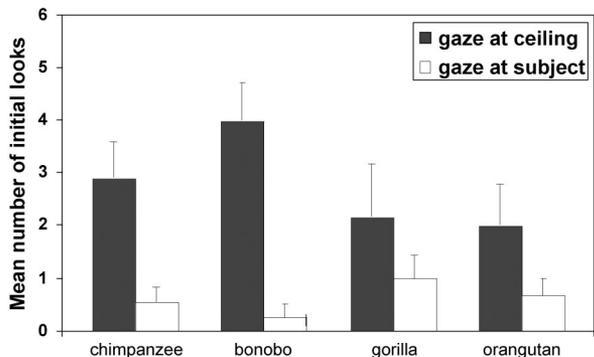


Figure 1. Mean number of initial looks in the two conditions: performance of the four species. Error bars represent standard error.

In contrast, age had a significant effect on the performance in the gaze-at-ceiling-condition, Kruskal–Wallis $\chi^2(2) = 5.95, p = .025$, one-tailed (see Figure 2). Adults were more likely to look up than infants in that condition (Mann–Whitney $U = 14.5, n1 = 7, n2 = 11, p = .027$).

However, age groups did not behave differently on the differential score, Kruskal–Wallis $\chi^2(2) = 3.16, p = .103$, one-tailed, or in the gaze-at-face conditions, Kruskal–Wallis $\chi^2(2) = 4.01, p = .135$.

Double looks. There was a significant difference in the number of double looks between the experimental and control conditions, Wilcoxon’s $T(N = 11) = 66, p = .003$. Subjects produced double looks in 23% of the cases in the experimental condition but never in the control condition. This effect was independent from species, Kruskal–Wallis $\chi^2(3) = 4.90, p = .18$, and sex, Kruskal–Wallis $\chi^2(1) = 1.41, p = .23$. In contrast, age had a significant effect on the amount of double looks, Kruskal–Wallis $\chi^2(2) = 7.90, p = .019$. Adults were more likely to engage in double looks than infants (Mann–Whitney $U = 14.0, n1 = 7, n2 = 11, p = .027$).

Because juveniles and adults produced more initial looks than infants, it is possible that the differences in double looking simply reflected the fact that these two age groups looked up more often in general. Therefore, we reanalyzed this data after correcting by the total number of looks in each age group (using

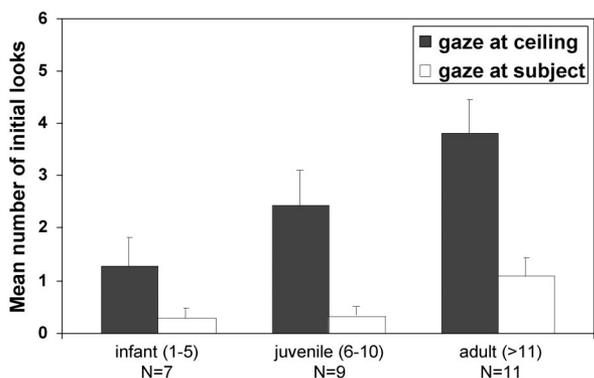


Figure 2. Mean number of initial looks in the two conditions: performance of the three age-groups. Error bars represent standard error.

a ratio based on the number of initial looks divided by the sum of double looks and initial looks). Figure 3 presents the distribution of double looks in relation to the number of initial looks across age groups. Again age had a significant effect, Kruskal–Wallis $\chi^2(2) = 7.28, p = .026$. This means that adults produced significantly more double looks than infants (Mann–Whitney $U = 5.0, n1 = 5, n2 = 9, p = .019$) even after controlling for the overall number of looks.

Discussion

Individuals of all four great ape species reliably followed the gaze of humans into empty space. There were no significant differences between species. These findings may not be surprising for bonobos and gorillas as they both live in social groups. The orangutans’ results, on the other hand, are more surprising as they are a semisolitary species, and presumably their social cognition might differ from that of the other more social apes. However, some researchers (Delgado & van Schaik, 2000; van Schaik, 2003) have argued that mean party size in orangutans remains small only because of the high costs of feeding competition. If the habitat is productive enough, they form parties that are comparable with the fission–fusion societies of chimpanzees. Moreover, it is suggested that the main benefits of grouping in orangutans are social (Delgado & van Schaik, 2000; van Schaik, 2003).

In addition to primates, other mammalian species can follow gaze—for example, goats (*Capra hircus*) follow the gaze of conspecifics to a location above and behind themselves (Kaminski et al., 2005). Also, dolphins (*Tursiops truncatus*; Tschudin, Call, Dunbar, Harris, & van der Elst, 2001) and South African fur seals (*Arctocephalus pusillus*; Scheumann & Call, 2004) follow gaze in object-choice situations. Although there was no evidence that dogs (*Canis familiaris*) follow human gaze outside of a simulated foraging context into free space (Agnetta, Hare, & Tomasello, 2000), they are very skillful in using human gaze in object-choice situations (Hare, Call, & Tomasello, 1998). Thus, it can be concluded that gaze following may be a skill shared by numerous social living animals.

Gaze-following behavior in the current study improved with age. Adults and juveniles were more likely to respond to the gaze of the human experimenter than the infants. This is consistent with other studies that have documented an improvement

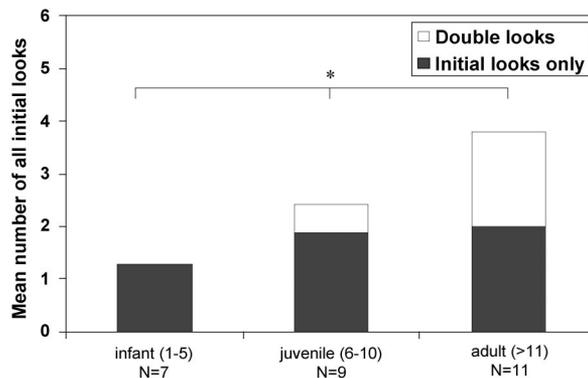


Figure 3. Rate of double looks within the mean number of all initial looks in the two conditions as a function of age. * $p < .05$.

in gaze-following behavior with age in rhesus macaques and chimpanzees (Okamoto et al., 2002; Tomasello et al., 2001). The infants in our study started to follow gaze at the age of 2.5 years, which is a bit earlier than in a similar study with chimpanzees (Tomasello et al., 2001), although Okamoto et al. reported that their chimpanzee subject reliably followed human gaze by 13 months of age. This age discrepancy may be explained by the methodological differences between studies. In particular, the experimenter in Okamoto et al.'s study looked at a specific object within the subject's visual field, whereas in the current study there was no object present and the experimenter directed her gaze outside the subject's visual field. Note that human infants also experience difficulty in gaze following if the target is outside their visual field. Thus, they improve their gaze-following skills so that by 12 months of age they are able to localize an object at which others are looking, but only by 18 months can they follow gaze into free space (Butterworth & Jarrett, 1991).

We found double looks in this study, thus replicating our previous results with a different group of chimpanzees (Call et al., 1998). This behavior never occurred in the control condition. One possible interpretation of double looks is that subjects expected to see what the experimenter was looking at, and therefore the gaze-following response involved more than a mere orienting response. However, there is an alternative that needs to be considered. Call et al. (1998) argued that after the initial look to the ceiling, subjects may have just returned to their normal visual orientation and the second look to the ceiling was simply a result of responding again to the head orientation of the human. If this were the case, this could be used to support the orienting-response model. However, there is an important piece of evidence that undermines this interpretation. The distribution of double looks is not a simple function of the initial looks, as the orientation-response model would predict, but it is age dependent. Double looks were never observed in infants and some were seen in the juveniles, but they represented about 35% of the initial looks in the adults. The shift in the rate of double looks suggests that apes first use gaze as a simple orientation cue, but later on they learn to use it in a more flexible way that involves appreciating that the partner is seeing something. This developmental change in double looks also fits with the changes observed in the development of gaze following discussed previously.

Moreover, it also fits the results of Tomasello et al. (2001), who found that adult chimpanzees, unlike infant chimpanzees, exposed to a human repeatedly looking to the same location (with no object present at that location) habituated and stopped producing gaze-following responses. The authors concluded that, in the period between infancy and adulthood, individuals come to integrate their gaze-following skills with their more general social-cognitive knowledge about other animate beings and their behavior and so become able to deploy their gaze-following skills in a more flexible manner. Taken together, these developmental patterns in habituation and double looks provide evidence for the perspective-taking model for adult individuals. Infants first might learn to use gaze for detecting something interesting, but later they develop a deeper understanding about the gaze of others as indicating that the looker sees something.

Experiment 2: Looking Around Barriers

The first experiment showed that great apes can follow the gaze of humans. Juveniles and especially adults of all four species exhibited double looks, providing support for the perspective-taking model. In a second experiment, we wanted to test the predictions of the two models further. In this study, a human experimenter looked around various types of barriers. The situation was such that the ape could not see what the human was looking at without changing her location. If, as predicted by the orientation-response model, the ape responded automatically to the human gaze she should orient in the same direction, observe the object the experimenter was looking at (e.g., the barrier), and stop. In contrast, if she was able to infer that the human was seeing something that she could not see, as predicted by the perspective taking model, she should move to a location from which she could see what the human was looking at.

Method

Subjects. We tested 6 orangutans, 4 bonobos, 6 chimpanzees, and 6 gorillas of various ages (range 3.5–30.0 years old) in this study. All of them except Ndiki and Nkwango had previously participated in Experiment 1 (see Table 1).

Materials. Testing took place in the same rooms as in Experiment 1.

Procedure. Each subject was tested individually and all apes stayed by themselves in their cage except for mothers with small infants (Fraukje, Natascha, and Dunja). We followed the procedure used by Tomasello et al. (1999). The experimenter sat in front of the ape in a specific place and fed food pieces to the ape. Suddenly, she looked to one of five predetermined locations (depending on the type of trial) for 1 min. In the control condition, the experimenter looked at the ceiling, whereas in the experimental condition, she alternated her gaze between the subject and one of four locations (but only one location per trial) corresponding to the following four types of barriers (see Figure 4):

Window: The window situated to the right of the ape (left side for the bonobos) was covered with paper and wood so that it was not possible to look through. The experimenter looked behind that covered window. The ape had to move behind and to the right (or left for the bonobos) to be able to see what the experimenter was looking at.

Door: The human access door to the testing room was half open so that the ape did not have a direct view to the corridor outside the room. The experimenter leaned back to look through the door into the hallway. To be able to see what the experimenter was looking at, the ape had to move approximately 2 m to the right (left for the bonobos).

Under: There was a frame on the cage between the wire mesh and the floor. Under that frame, there was a small gap of approximately 2 cm. The experimenter looked down on his side of the wire mesh, where, in some cases, a grape or a piece of banana was placed. To be able to see what the experimenter was looking at, the ape had to lean down and look through the gap.

Under left: There was a frame to the right of the ape's location in the cage. Under that frame, there was a small gap of approximately 2 cm. The experimenter looked diagonally under this frame, where, in some cases, a grape or a piece of banana was placed. To be able to see what the experimenter was looking at, the ape had to get near to the frame.

After 1 min had elapsed, the experimenter ceased her looking behavior and gave a piece of food to the subject. This was completely independent from what the ape had done during the trial. We gave each subject three

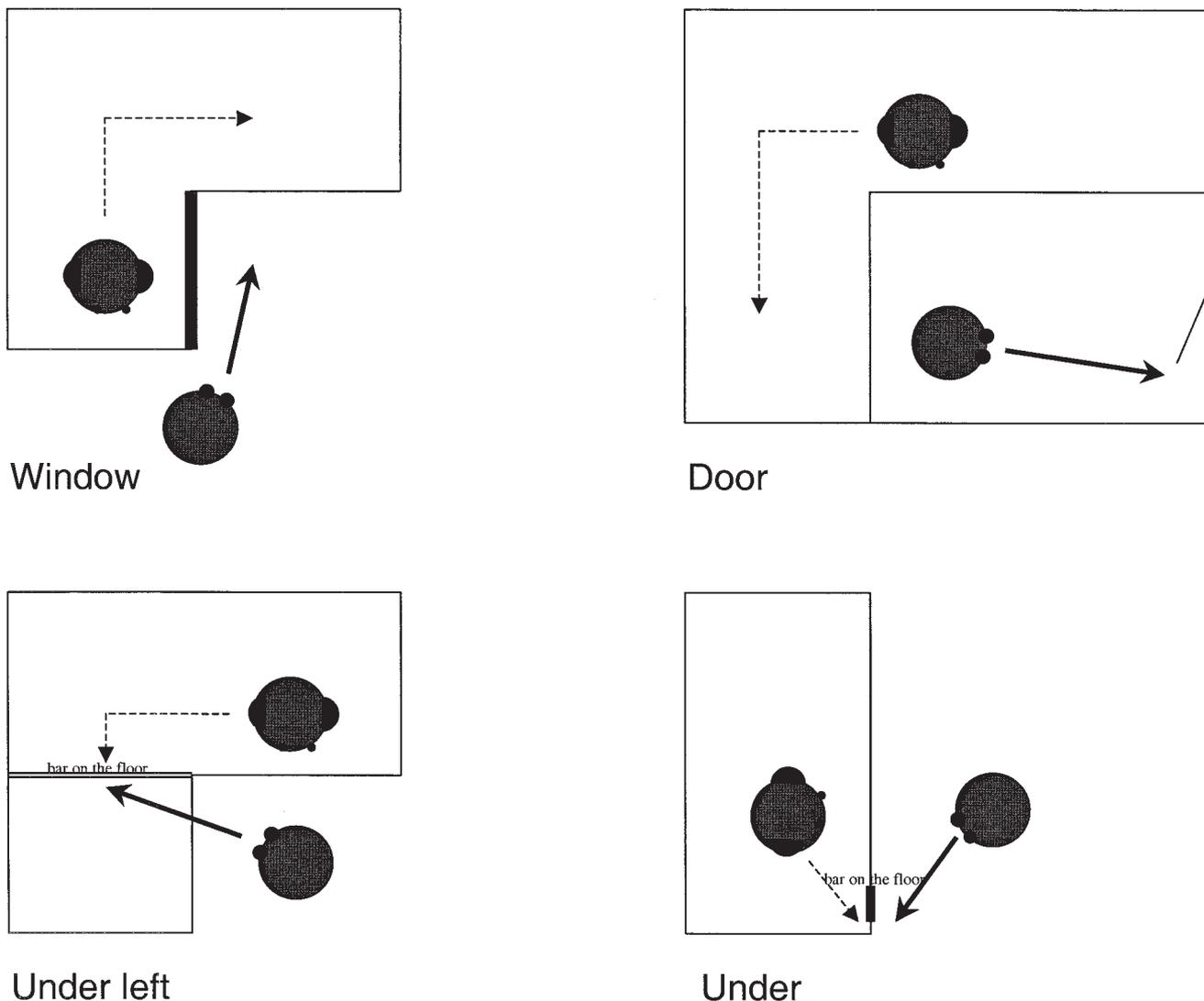


Figure 4. Diagram of the four different types of barriers used in Experiment 2 showing the experimenter's location, the ape's starting location, and the ape's target location indicated by the dashed arrow. Two of them took place in one part of the cage (door and under left; for the bonobos door and window), and two of them in the other part (window and under; for the bonobos under and under left).

experimental trials and three control trials per type of barrier, so that each subject received a total of 24 trials. Each experimental trial was paired with a control trial that was conducted before or after the experimental trial. A session consisted of four trials (two experimental and two corresponding control trials), which meant that each subject was tested for six sessions. Because the motivation of the apes to react seemed to decrease quickly, we introduced intertrial periods (at least 1 min within a experimental-control pair and at least 10 min between two experimental conditions) in which the experimenter fed the apes and played with them. To minimize habituation, we allowed a break of at least 5 days between the sessions.

Scoring

All trials were scored from the videotapes. The trials were filmed so that the target location where the ape was expected to be was visible. Because of the arrangement of the room, it was not always possible to

see where the apes were looking at precisely. Therefore, we measured two variables. One variable was whether the ape visited the target location from where she would be able to see what the experimenter was looking at. The use of this measure meant that subjects had to move to those locations to see what the experimenter was looking at in three of the four conditions. The other variable was the time (in seconds) subjects spent at the location where she would be able to see what the experimenter was looking at. The specific criteria for the different types of barrier were as follows (see Figure 4):

Window: The tape showed an area right of the covered window that was approximately 1 m wide and 1 m high. We coded whether and how long the subject would stay in that area with both eyes visible.

Door: The tape showed a window with its frame. Sitting in front of that window, the ape was able to look through the crack of the door.

We measured whether and how long the subject would stay in that area having crossed the frame with at least one part of the body.

Under: The tape showed the area of 1 m × 1 m down in front of the ape. We measured whether the subject would stay in that area close to the experimenter during the whole trial of 1 min. Also, we measured how long the subject would stay in that area.

Under left: The tape showed the area around the frame that was to the right of the ape. We measured whether and how long the subject would stay near to the frame.

All tapes were coded by one experimenter. As was the case in the previous experiment, we also calculated the difference between the experimental conditions to analyze the effect of species, sex, and age. A second independent observer coded 20% of the trials to assess interobserver reliability. Interobserver reliability for the frequency of visits to the target location and the duration at the target location was excellent (frequency: $\kappa = 0.93$; duration: Pearson's $r(116) = .98$). We used nonparametric statistics because the homogeneity of variance assumption was violated.

Results

Number of stays at the target location. Figure 5 presents the mean number of stays at the expected place for the four species after collapsing all types of barriers. Overall, subjects visited the expected place significantly more often in the experimental condition compared with the control condition, Wilcoxon's $T(N = 15) = 100.0, p = .021$. We found no significant differences across species on the difference between experimental and control conditions, Kruskal–Wallis $\chi^2(3) = 1.20, ns$, although species might have differed if the control condition is considered alone, Kruskal–Wallis $\chi^2(3) = 7.60, p = .055$. Likewise, neither sex nor age had a significant effect on the difference between the experimental and control conditions—sex, Kruskal–Wallis $\chi^2(1) = 0.29, ns$; age, Kruskal–Wallis $\chi^2(2) = 0.45, ns$.

Figure 6 presents the mean number of stays for each of the four types of barriers. There was a significant difference between experimental and control condition for under left, Wilcoxon's $T(N = 12) = 72.5, p = .005$, but not for under, Wilcoxon's $T(N = 8) = 22.5, p = .48$, window, Wilcoxon's $T(N = 6) = 10.5, p = 1.0$, or door, Wilcoxon's $T(N = 12) = 53, p = .25$.

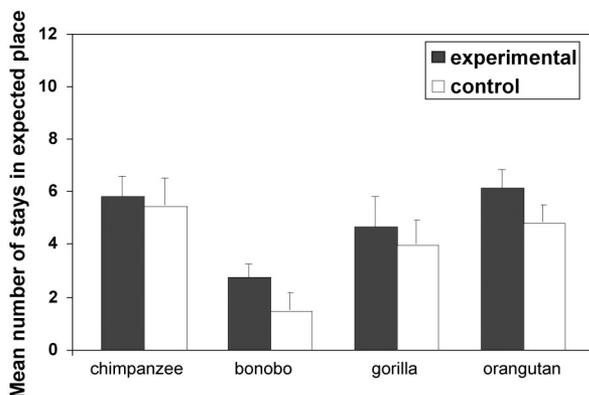


Figure 5. Mean number of stays in the expected place for all barrier types: performance of species in experimental and control conditions. Error bars represent standard error.

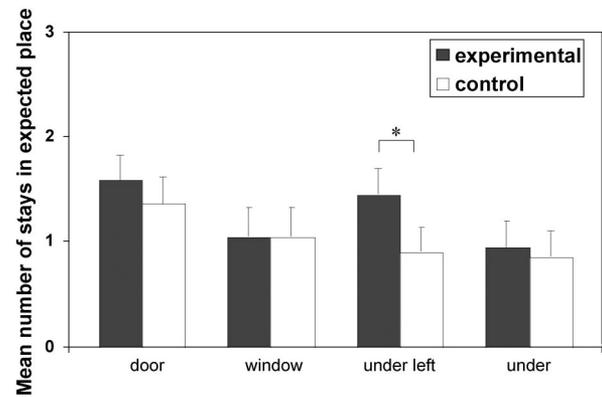


Figure 6. Mean number of stays in the expected place: performance in the four barrier types in experimental and control conditions. Error bars represent standard error. * $p < .05$.

Duration of stays at the target location. Overall, subjects stayed longer at the target location in the experimental condition compared with the control condition, Wilcoxon's $T(N = 20) = 184.5, p = .003$. There were no differences of this effect for the different species, Kruskal–Wallis $\chi^2(3) = 3.12, p = .37$, two sexes, Kruskal–Wallis $\chi^2(1) = 3.29, p = .070$, or three age classes, Kruskal–Wallis $\chi^2(2) = 4.12, p = .13$.

Figure 7 presents the mean duration of stay at the target location for each of the four types of barriers. There was a significant difference between experimental and control conditions for under, Wilcoxon's $T(N = 18) = 141.5, p = .015$, and under left, Wilcoxon's $T(N = 16) = 115, p = .015$, but not for window, Wilcoxon's $T(N = 13) = 57, p = .42$, or door, Wilcoxon's $T(N = 17) = 98, p = .31$.

Discussion

Presented with several situations in which the human experimenter looked behind some kind of barrier, apes overall went more often to the locations from which they could see what the experimenter was looking at than they did when the human looked at the ceiling (control condition). Moreover, subjects stayed longer in

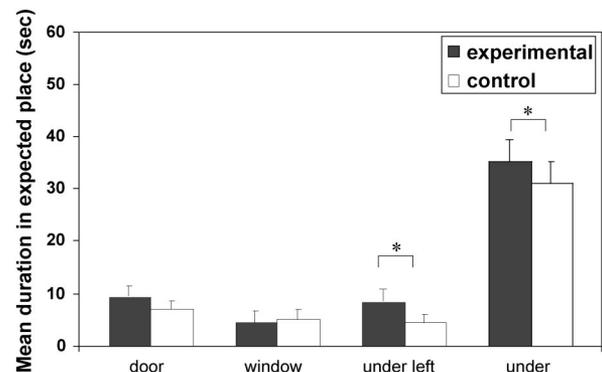


Figure 7. Mean duration in the expected place: performance in the four barrier types in experimental and control conditions. Error bars represent standard error. * $p < .05$.

these locations in the experimental condition compared with the control condition. There was no difference in performance across species, age, or between sexes. This effect was also noticeable for some specific barriers when they were analyzed separately. In one type of barrier (under left) the apes more often visited the location from which they could see what the experimenter was looking at, whereas in two conditions (Under and under left) the apes stayed longer in that location.

Although these results replicate previous findings with chimpanzees (Tomasello et al., 1999), the magnitude of the effect, especially considering the different types of barriers individually, is rather weak. One explanation is that the situation with a human experimenter is quite artificial for an ape. Tomasello et al. (1999) suggested that studies in which primates do not follow the gaze direction of humans may reflect more of a motivational problem than a competence problem because primates are much more interested in where conspecifics are looking than in where humans are looking (Itakura, Agnetta, Hare, & Tomasello, 1999). Although in our first experiment the apes responded to human gaze, in most cases within the current study they had to move to see what the experimenter was looking at. So the costs to respond were much higher whereas the benefit was low—no food was available for them during the trial when the human experimenter gazed at a certain place for 1 min. Therefore, it might have been a motivational problem.

However, Tomasello et al. (1999) also used human experimenters to convey information in the absence of food, yet subjects responded more to the human experimenter than in the current experiment. Several methodological differences may explain this discrepancy between studies in the degree of gaze following elicited by our situation. First, it might be possible that our independent measure was not sensitive enough. Because of the arrangement of the room, we could not always see where the apes were looking. That is why we defined a place where it was certain that the ape was able to see what the human was looking at. We then coded the number and the duration of the stays in that expected place. This might not be the best measurement to find out whether the apes responded to the human gaze. Second, the human experimenter in the Tomasello et al. (1999) study produced vocalizations that might have increased the attention of the tested chimpanzees, whereas in the current study there were no vocalizations. This idea is supported by some data showing that adding vocalizations enhances the subjects' performance in an object-choice paradigm (Call, Agnetta, & Tomasello, 2000). Third, the types of barriers were not identical between the two studies because of the constraints imposed by the different caging setup in the two study sites. It is possible that the apes responded more in those situations in which the human looked at a place where they expected to see something interesting that could be reached (e.g., food). In fact, the two barriers that elicited the strongest response were those in which the human looked under the bar of the cage (i.e., the under and under left conditions), perhaps precisely because in these situations they would have been able to reach any food that might be there.

General Discussion

All four great ape species can follow a human's gaze both to distant locations and around barriers. Individuals of all four species

reliably followed the gaze of humans into empty space and sometimes double checked where the human experimenter was looking. Moreover, there was an improvement with age that may suggest that apes first used gaze as a simple cue, but later on they learned to use it in a more flexible way. In the second experiment, the apes had to move if they wanted to track the human gaze. It turned out that the apes stayed more often and longer in the places from which they could see what the experimenter was looking at than they did in the control condition in which the human looked at the ceiling.

These results disconfirm the orienting-response model and are consistent with the perspective-taking model. The apes did not respond automatically to the human gaze as a cue. First, and of most importance, individuals of all four species were able to change position to check the place where the human was looking, and they did not just stare at the opaque object at which the human was looking (i.e., the barrier). In addition, apes produced double looks presumably because they expected to see what the human was looking at. This ability, like gaze following itself, followed a clear developmental trajectory. Double looks were absent in infants, appeared infrequently in juveniles, and were more common in adults. Because of these two findings, we can conclude that apes are able to track the human gaze geometrically and appreciate that the partner is seeing something.

These positive results contrast with those of the object-choice studies in which apes are much less skilful at using gaze to select the baited container from two available containers. The discrepancy between being able to follow human gaze but not being able to use it to select the baited container is puzzling (Call et al., 1998; Itakura et al., 1999). One possible explanation for this discrepancy is that a simple gaze cue by itself is not enough to suggest the presence of food in the gazed-at locations. Call et al. (1998; see also Tomasello et al., 1999), argued that chimpanzees may follow gaze to the baited container as some studies suggest for monkeys (e.g., Emery et al., 1997), but on seeing the container, which was not an unusual sight as they had seen it on the platform the whole time during the trial, they then selected randomly. Tomasello (1999) argued that this could be interpreted as evidence that they lack a deep understanding of the communicative intentions of others. It is conceivable that, to fully exploit this information, some other behavioral or contextual cue must also be present. In fact, Call et al. (1998) found that chimpanzees can use a human's gaze direction to choose a tube or barrier containing food. In that case, the human had visual access to the food while giving the cue. The authors suggest that the chimpanzees either understood the physical properties of these occluders (i.e., that the experimenter could see the food but they could not) or they used the orientation of the human. That idea fits with the current results. So these contextual cues would supply the scaffolding necessary for successful performance in object choice in the absence of communicative intentions.

It is interesting to note that domestic dogs (*Canis familiaris*) can use gaze and various other cues to locate hidden food in an object choice task (Hare et al., 1998; Hare & Tomasello, 1999; Miklosi et al., 1998; Soproni, Miklosi, Topal, & Csanyi, 2001). Moreover, dogs that had little human contact show this skill whereas wolves (*Canis lupus*) do not. These findings suggest that dogs do not have to learn these cues and have been selected for their abilities to communicate with humans in a unique way (Hare, Brown, Wil-

liamson, & Tomasello, 2002). However, another study has shown that when wolves experience the appropriate rearing conditions, they can learn about human cuing (Miklosi, Kubinyi, Gacsi, Viranyi, & Csanyi, 2003). Actually, enculturated apes that grew up with much human contact show a better performance in an object-choice design (Call et al., 2000; Itakura et al., 1999; Itakura & Tanaka, 1998). Moreover, it was shown that chimpanzees, orangutans, and gorillas can learn to use social cues like gaze to locate hidden food in this task (Itakura & Tanaka, 1998; Peignot & Anderson, 1999). Similarly, fur seals and dolphins with extensive contact with humans are also able to use gaze to locate the target container (Scheumann & Call, 2004).

We also cannot rule out that the apes used body and head orientation in addition to gaze. In particular, we do not know whether individuals used head direction in general or something more specifically with the eyes. However, we know that at least chimpanzees can follow human gaze when the human just moves her eyes without movement of the head (Povinelli & Eddy, 1996). On the other hand, as mentioned above, we know that chimpanzees do not use stronger behavioral cues like pointing, touching, and lifting the cup to locate hidden food in an object-choice task (Call et al., 2000; Itakura et al., 1999). In other words, it is quite unlikely that the apes in our study moved because they simply used behavioral cues of the human experimenter when they do not do that in a situation in which food is hidden. It is more likely that they really tracked the human gaze.

In conclusion, apes are able to track gaze reliably to hidden targets and look back to the human experimenter when they do not find a target. This suggests that their gaze following is not just an orienting response. But it may involve some perspective-taking skills. These results together with recent studies on food competition (Hare, Call, Agnetta, & Tomasello, 2000) and gestural communication (Liebal, Pika, Call, & Tomasello, 2004; Kaminski, Call, & Tomasello, 2004) suggest that apes have an appreciation of what others can and cannot see. Since all great apes display those skills it is conceivable that they were also present in their common ancestor. Whether other nonhuman primates and other animals also possess the same level of sophistication in perspective-taking abilities remains to be seen. It would not be surprising to find that these skills are widespread in animals with a complex social environment. In fact, there is considerable evidence that dogs can take the human perspective in both communicative and competitive situations (Bräuer, Call, & Tomasello, 2004; Call, Bräuer, Kaminski, & Tomasello, 2003; Viranyi, Topal, Gacsi, Miklosi, & Csanyi, 2004).

When tested in a setting similar to the current study, common ravens (*Corvus corax*) follow the gaze direction of humans around obstacles as well. The ravens were already capable of simple gaze following as fledglings, but they consistently tracked human gaze only when they reached independence. The authors of that study suggested a hybrid explanation: Individuals have a natural tendency to follow the gaze of others and also learn about the differential significance of gaze in different physical conditions (Bugnyar, Stöve, & Heinrich, 2004). This could also be true for the apes. Whether apes have a natural tendency to follow gaze and then learn about gaze direction, or whether their skills of visual perspective taking entail other complexities from the outset, is a matter for further studies.

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