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Chimpanzees, *Pan troglodytes*, follow gaze direction geometrically

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Two experiments on chimpanzee gaze following are reported. In the first, chimpanzee subjects watched as a human experimenter looked around various types of barriers. The subjects looked around each of the barriers more 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 towards the back of their cage. As they turned to follow the human's gaze a distractor object was presented. The chimpanzees looked at the distractor while still following the human's gaze to the back of the cage. These two experiments effectively disconfirm the low-level model of chimpanzee gaze following in which it is claimed that upon seeing another animate being's gaze direction chimpanzees simply turn in that direction and look around for something interesting. Rather, they support the hypothesis that chimpanzees follow the gaze direction of other animate beings geometrically to specific locations, in much the same way as human infants. The degree to which chimpanzees have a mentalistic interpretation of the gaze and/or visual experience of others is still an open question.

Many primate species visually track the gaze direction of conspecifics to outside entities. Solid experimental evidence exists for chimpanzees, sooty mangabeys, *Cercocebus torquatus*, and three species of macaque, *Macaca mulatta*, *M. nemestrina*, *M. arctoides* (Tomasello et al. 1998). Chimpanzees also visually follow the gaze direction of human beings to outside entities. They do this on the basis of eye direction alone independent of head direction (Povinelli & Eddy 1996), even when the target is located above and/or behind them (Itakura 1996; Povinelli & Eddy 1997; Call et al. 1998). Gaze following is not confined to primates, however, as many domestic dogs, *Canis familiaris*, reliably track human gaze direction under experimental conditions as well (Miklósi et al. 1998; Hare & Tomasello 1999; Hare et al., in press). Following the gaze direction of conspecifics is presumably useful in helping chimpanzees and other primates to locate such things as food, predators, or groupmates engaged in significant social interactions.

From a cognitive point of view, the question is how chimpanzees understand the visual gaze of other animate beings. There are two major possibilities: the so-called 'low-level' and 'high-level' models. In the low-level model, chimpanzees have a tendency to look in the direction that others are looking (ontogenetic mechanism unknown). When they do this they quite often see interesting and important events and objects in the environment, and so they learn that the gaze direction of others is a reliable cue for such things. In this model, then, the cognitive process is something like: look in the direction others are looking until you see something interesting, at which point you should stop. In the high-level model, on the other hand, a chimpanzee at some point comes to understand that when other individuals look in a direction they are seeing something, that is, they are having some kind of mental experience. In this model, then, the cognitive process is something like: look in the direction others are looking and you will see what they are seeing.

Some recent evidence supports the low-level model. The main finding is that chimpanzees follow human gaze direction in the so-called object choice paradigm, but they do not seem to know what that gaze direction means. In this procedure, a human experimenter hides food in one of two containers, provides a cue such as gaze direction indicating the location of the food, and then gives the subject a choice of containers (Anderson et al. 1995). In a number of studies, chimpanzees have failed to take advantage of gaze direction to find the hidden food (e.g. Tomasello et al. 1997; Itakura et al., in press). Povinelli et al. (1999) found that some chimpanzees could use gaze direction cues in this paradigm, but a variety of lines of evidence led to the interpretation that

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the subjects were using it as a simple discriminative (arbitrary) cue, not as evidence for mental states (see also Povinelli & Eddy 1997; Call et al. 1998; Itakura & Tanaka 1998). These studies are consistent with the low-level model since the chimpanzees follow human gaze to the correct container (an interesting object) and then terminate their search without understanding that the food they are seeking is inside that container.

There is one finding, however, that may be consistent with the high-level model. Povinelli & Eddy (1996) had a human experimenter face a chimpanzee as it entered a test room to beg for food through a Plexiglas wall. The experimenter then immediately stared in a particular direction. In his line of sight was a solid partition affixed to the Plexiglas wall. If the partition had not been there, the experimenter's focus would have been to the back wall of the room, behind the subject. The reasoning was that if the chimpanzees were simply using gaze direction as a cue that something interesting was somewhere along the human's line of sight, they should follow that line of sight all the way to the rear of the room. However, if they stopped and inspected the partition (i.e. the human's side), the inference was that they must know that the human's sight to the rear of the room was blocked and that she was looking at something on her side of the partition. Results showed that the chimpanzees did look at the partition more than they looked at the back wall. However, it is possible that the chimpanzees simply saw the partition as an interesting object in its own right, and so stopped when they saw it (Tomasello & Call 1997). The key in making the more high-level interpretation of this study would be attempts by the chimpanzees to look at the human's side of the partition, since this would demonstrate an appreciation for precisely what the human was seeing. Unfortunately, although Povinelli & Eddy reported the occurrence of this behaviour, there was no statistical comparison of the subjects' looks to the experimenter's and their own side of the partition.

In the current study, we attempted to follow Povinelli & Eddy's (1996) experimental strategy but in a more systematic way. In the first experiment, we presented chimpanzees with a series of four situations in which a human experimenter looked behind some kind of barrier. The question was whether the subjects would move themselves (which was required in all cases) so that they could see what the human was seeing. In the second experiment, we presented chimpanzees with a human looking towards the back of their cage. The key point was that in one condition there was an intervening object (distractor) that the subject would see if it turned to follow the human's gaze to the back of the cage. The low-level model predicts that the subject should terminate its search at this point (it has found an interesting object), whereas the high-level model predicts that at least some of the time the subject should either ignore the distractor object and look directly at the back of the cage where the human was looking, or else look at both places. If in these two experiments, chimpanzees were to follow human gaze direction, that is, both behind barriers and past distractors, this would provide very strong evidence against the low-level model of chimpanzee gaze following and at least some evidence in the direction of the more high-level model.

EXPERIMENT 1

We first investigated whether chimpanzees will look around a barrier immediately after a human experimenter does so, seemingly attempting to see what he is seeing.

Methods

Subjects

The subjects were 14 male and female chimpanzees at the Yerkes Primate Center Field Station. Their average age was 17.5 years, with 10 adults (average age 23 years) and four infants (average age 4 years). Each of the four infants belonged to one of the adult subjects and so lived with, and was tested with, its mother. All subjects were housed in small group cages with indoor and outdoor areas, both ca. 3 m^3. Testing took place in the indoor areas, each of which had three solid walls and a fourth wall of wire caging facing the hallway for caretakers. The subjects were fed on their normal diet (chow and fruit) and normal schedule throughout testing.

Materials and design

Each subject was tested individually for its tendency to follow a human experimenter's (E's) gaze around a barrier. There were four different kinds of barriers (Fig. 1), with each used in both experimental and control trials.

(1) Gutter: a desirable food (e.g. grapes) was placed in a drainage gutter at one of the front corners of the subject's cage. The subject could see inside the gutter only by approaching it and bending down appropriately (a trial was begun only when the subject was near the middle of the cage). In experimental trials, E simply looked into the gutter, which was visually accessible from his vantage point just outside the cage. In control trials, E looked towards the top corner of the cage away from the gutter containing the food.

(2) Board: a board was placed just outside the subject's cage, standing at an angle relative to the subject. A desirable food (e.g. grapes) was placed on E's side of the board, so that the subject could see it only by moving to the front and far side of the cage (putting its head very close to the side wall of the cage), or by climbing the wire fencing that constituted the front wall of the cage to ca. 1 m high (a trial was begun only when the subject was near the middle of the cage). In experimental trials, E simply looked towards the food behind the board. In control trials, E looked towards the top corner of the cage away from the board.

(3) Rooms: a door in one side wall was opened, giving subjects access to the adjoining cage (empty). The door was located approximately in the middle of the wall, so that when the subject was near the front of the cage it would have to go backwards to look through the door (a trial was begun only when the subject was near the front of the cage, against the wall separating the two cages). In experimental trials, E simply looked into the adjoining

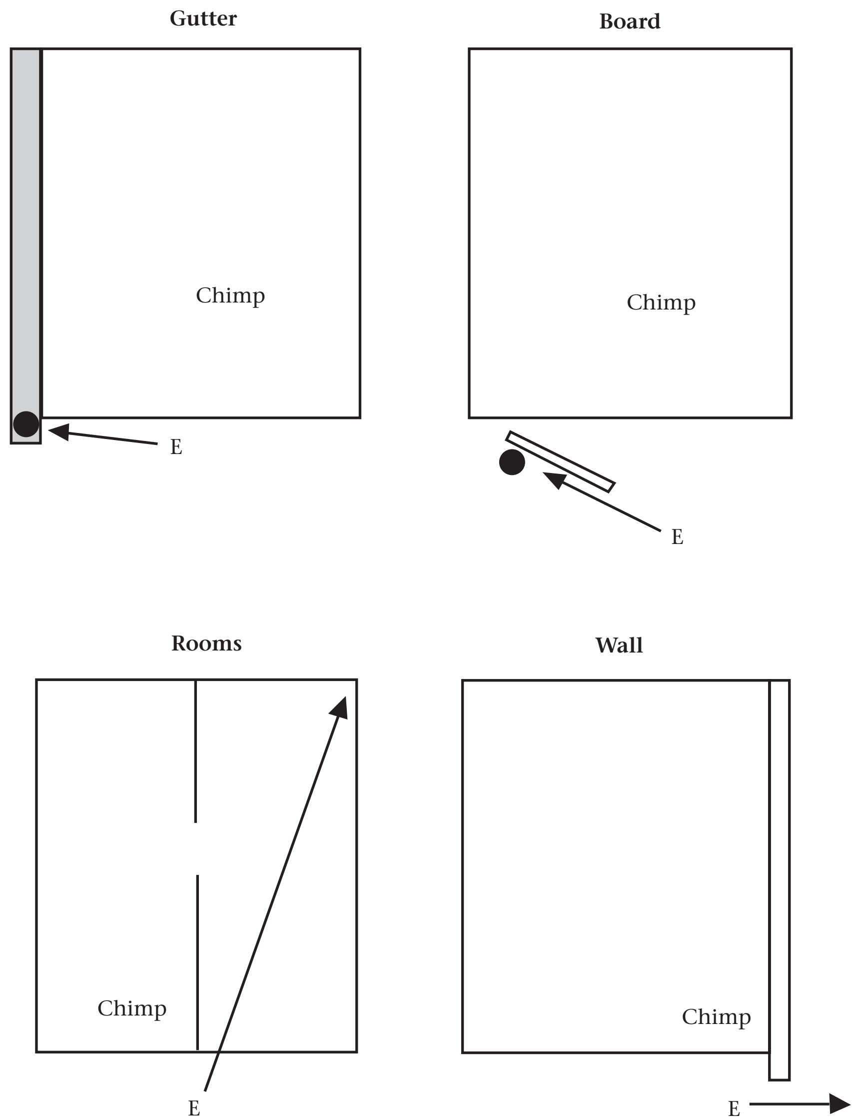

Figure 1. Layout of the four barrier situations in experiment 1. Arrows indicate where the human E looked in each experimental condition (the control was to the opposite side of the room). 'Chimp' indicates where the subject began each trial. Closed cicles indicate placement of food.

room (top back corner). In control trials, E looked towards the top corner of the cage away from the adjoining room. There was no food in these trials.

(4) Wall: the side wall of each cage extended about 1 m into the hall beyond the wire caging, providing a natural barrier if the chimpanzee attempted to look down the hallway from close to the wall. By moving closer to the centre of the front wall of the cage (or far side) chimpanzees could see some way down the hall. In experimental trials, E simply looked down the hallway (a trial was begun only when the subject was near the front of the cage and to the side E was going to look down, requiring the subject to move away and look back down the hall). In control trials E looked towards the top corner of the cage away from the wall the subject was close to. There was no food in these trials.

We gave each subject 12 experimental trials and 12 control trials, three of each for each type of barrier. Each subject was tested in three 1-day sessions, each of which consisted of one experimental and one control trial for each of the four barriers (paired together, for a total of eight trials). The order of experimental and control trials was counterbalanced within subjects, so that each subject had an equal number of trials in which experimental and control trials were administered first (with the type of initial trial in the initial session counterbalanced across subjects). The order of barriers was constant across sessions for a given subject, but roughly counterbalanced across subjects (four different orders were used, with approximately equal numbers of subjects in each order). Each of the three testing sessions took place on a different day. To minimize habituation to the barriers, the three different sessions for a given subject were administered ca. 1–2 weeks apart.

The six adult chimpanzees that did not have infants were tested alone. The four adult subjects with infants were tested together with their infants; that is, E waited until both subjects were located and attending

Table 1. Number of trials in which subjects looked around a barrier as the human experimenter was doing

	Gutter		Board		Rooms		Wall		Total	
	Experiment	Control	Experiment	Control	Experiment	Control	Experiment	Control	Experiment	Control
Ericka	2	0	2	0	0	0	0	0	4	0
Jesse	0	0	1	0	0	0	0	0	1	0
Cici	0	0	0	0	2	0	1	1	3	1
Sonia	0	0	0	0	1	0	2	0	3	0
Vivian	0	0	0	0	1	0	1	1	2	1
Buffy	0	0	0	1	0	0	0	0	0	1
Tai	0	0	1	0	1	0	2	0	4	0
Barbara	0	0	0	0	0	0	0	0	0	0
Sheila	0	0	0	0	2	0	1	0	3	0
Magnum	0	0	0	0	0	0	1	0	1	0
Jamie (I)	1	0	2	0	1	0	2	0	6	0
Dover (I)	2	1	1	1	2	1	0	0	5	3
Stuart (I)	3	0	2	0	0	0	0	0	5	0
Abbey (I)	1	0	0	0	0	0	1	1	2	1
Total	9	1	9	2	10	1	11	3	39	7

The values represent the sum for each individual across three sessions; thus, the total number possible in each cell is 3. I: Infants.

appropriately (typically child in contact with but in front of its mother) and then gave the appropriate cues for both.

Procedure

The same human experimenter (E) ran all trials, which were videotaped for later analysis. The video camera was positioned in the hallway behind the experimenter, filming the subjects through the wire caging.

E began a given trial when: (1) the subject was positioned appropriately for the particular barrier type (see above); and (2) the subject was looking towards E. E then gave the appropriate gaze cue for the particular barrier and condition involved (see above). The cue was given repeatedly for 1 min; that is, E alternated his gaze between the subject and the target location for 1 min. E stayed in the same basic location for a given trial (see Fig. 1), although he sometimes moved closer to or further from the subject, or went from sitting to standing and vice versa, to maintain attention (he never moved left or right). E oriented his body directly towards the subject throughout the 1 min; to give the cue he simply moved his head and eyes in the appropriate direction (with as little torso involvement as possible). For the middle session only, E also produced vocalizations (human approximation to a chimpanzee pant-grunt) during each trial in order to maintain attention. Approximately 5–10-min breaks were taken between pairs of trails (i.e. an experimental and control trial for a given barrier were given in relatively immediate succession, and then a break was taken before proceeding to the next pair of trials for the next barrier).

Scoring

All trials were scored from the videotapes by E. For all experimental trials, subjects had to move their bodies and their heads in particular ways to be able to gain visual access to the location E was seeing, differently for each barrier. Each trial was scored for whether the subject moved its body in an apparent attempt to see around the barrier, that is, to gain visual access to whatever E was looking at (control trials were scored in this same way; they were not scored for whether the subject followed E's gaze to the control location). The specific criteria for the different barriers were as follows.

(1) Gutter: the subject had to approach the gutter, look down into it by bending down close to the ground, and actually retrieve the food.

(2) Board: the subject had either (a) to come to the front and side of the cage and then look around the board, or (b) to climb the caging ca. 1 m high to look over the board.

(3) Rooms: the subject had to move back to the open door and either (a) look through it while remaining in its cage, or (b) move into the adjoining cage while looking towards the far top corner at which E had been looking.

(4) Wall: the subject had to move away from the side wall and look back around that wall, down the hallway.

To assess interobserver reliability, a random sample of 48 of the 336 total trials (14%) were scored by a second independent observer (approximately equal numbers of trials from each barrier type and for experimental and control trials). There were four disagreements, for a percentage agreement score of 92%.

Results

Table 1 gives the results for each subject in each barrier situation. Summing across individuals it is clear that subjects looked around the barrier more in the experimental than in the control situation for each barrier situation individually: nine to one for the gutter (binomial test: $P<0.05$), nine to two for the board ($P<0.05$), 10 to one for the rooms ($P<0.01$) and 11 to three for the wall ($P<0.05$). Summing across individuals and barrier types the result is 39 to seven ($P<0.001$). If subjects are analysed individually, about half showed a strong tendency to look around the barrier reliably in the experimental condition but not in the control condition (3 to 0 or better). The middle session did not produce different results from the other two, suggesting that the vocal accompaniment to the gaze cue had no dramatic effects. Subjects did not follow the gaze more often in the two conditions involving food (Gutter, Board) than in the two that did not (Wall, Rooms; paired *t* test: t_{13}=0.49, NS).

There was a very strong tendency for the infants to follow E's gaze around the barrier. Even though there were only four infants, they had a total of 18 looks in the experimental condition and four in the control condition, while the 10 adults' comparable figures are 21 and three, indicating that on average the infants looked around the barrier in the experimental condition more than twice as often as the adults. Two of the infants (Jamie and Stuart) are among the most reliable individuals in the entire sample.

Discussion

For each of the four barriers separately, chimpanzees looked around the barrier more in the experimental than in the control condition. Summed across the four barriers the results are even stronger, with subjects looking around the barrier about five to six times more frequently in the experimental than in the control condition. From the point of view of individuals, about half the sample showed fairly clear signs of looking around the barrier more often in the experimental than control condition. This was true for both the adults and the infants, and indeed, on average, the results for the infants were stronger than they were for the adults. The results are no stronger for the two conditions in which food was involved; this suggests that the motivation to follow the gaze is not driven only by the material rewards to which it might lead.

These results are clearly discrepant with the low-level model of chimpanzee gaze following. In this model, chimpanzees should look in the direction in which E is looking, and then when they encounter the barrier look at it (from their own side), if indeed they find it interesting. If they do not find the barrier interesting they should continue to look along E's line of sight or they should stop looking altogether. It is still not clear, however, if one must invoke the high-level model to explain these results. In fact, in studies with human infants, Butterworth & Jarrett (1991) have called this kind of gaze following around barriers and the like 'geometric', as it requires that the subject actually project a line of sight for the other person into the distance. But one may project a line of sight for another being without attributing to them any intentional or mental states.

EXPERIMENT 2

In experiment 2, we used a different method to evaluate the different models of chimpanzee gaze following. The logic was as follows. If the low-level model is correct, when chimpanzees turn in the direction of E's gaze they should stop at the first interesting object they see. On the other hand, if they are tracking E's line of gaze geometrically, they should not be deterred by other distracting objects they see along the way, but rather should track E's gaze past such distractions. In experiment 2, therefore, E looked towards the back of the cage but another moderately interesting object was placed so that the subject would see it first, before it could see the back of the cage where E was looking. Needless to say, the salience and attractiveness of the distractor object is an important issue in this experimental design because this object had to be salient and attractive enough to attract the subject's attention in the first place (or else it would not be a distraction), but not so salient and attractive that the subject would lose all interest in what E might be looking at.

Methods

Subjects

Ten adult chimpanzees served as subjects, nine of whom also participated in experiment 1. Their average age was 21 years (range 9–38). The overall housing, feeding and testing situations were the same as in experiment 1. (This experiment was actually done first.)

Materials and design

Each subject was individually tested for its tendency to follow a human experimenter's (E1's) gaze in each of three experimental conditions (Fig. 2). Also present in some conditions was a second human experimenter (E2).

(1) Target only: E1 looked towards the top and back of the cage on the side wall furthest from the subject. E2 was not present and no distractor object was present, nor was there an actual object that was the target of E1's look.

(2) Distractor only: E1 looked sideways towards a brightly coloured and novel toy doll (5 × 3 cm) that E2 was holding and lightly shaking.

(3) Target with distractor: E1 looked towards the top and back of the cage on the side wall furthest from the subject (as in Target only condition). In this case, however, E2 held and shook the doll (as in the Distraction only condition) in such a way as to attract the subject's attention as it turned to follow E1's gaze.

Each subject was given 18 experimental trials, six in each of the three experimental conditions. Each subject was tested in six 1-day sessions, each of which consisted of one trial from each of the three experimental conditions. The order of experimental conditions was completely counterbalanced within subjects, so that each subject experienced each of the six possible orders of three experimental conditions once. Direction of gaze was also completely counterbalanced within subjects so that each subject received nine trials in which E1 looked to the left and nine trials in which E1 looked to the right (three in each condition). Each of the six test sessions took place on a different day. To minimize

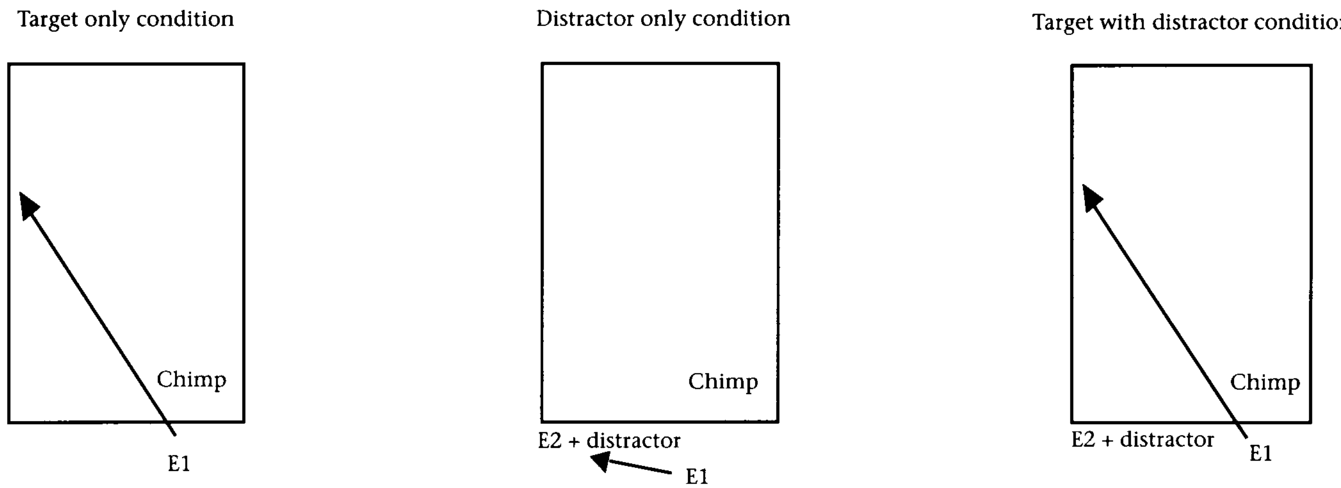

Figure 2. Layout of the three experimental conditions in experiment 2. 'Chimp' indicates where the subject began each trial. E1 is the first human experimenter; arrows indicate where he looked in each experimental condition. E2 is the second human experimenter who held a distractor (a novel doll).

habituation to the procedure, these sessions were administered for a given subject ca. 1 week apart, with all subjects completing the entire procedure within a 10-week period.

Procedure

The same human experimenters (E1 and E2) ran all trials, which were videotaped for later analysis. The video camera was positioned in the hallway behind E1, filming the subjects through the wire caging.

E1 began each trial by enticing the subject (sometimes with food) to the front and side of the cage (either left or right). He then secured the subject's attention and looked in the way appropriate for the experimental condition (see above). In all cases E1 looked repeatedly for 15–20 s; that is, he alternated his gaze between the subject and the appropriate location. He stayed seated in the same basic location for a given trial (see Fig. 2, either right or left) and he oriented his body directly towards the subject throughout the 15–20 s; to give the cue he simply moved his head and eyes in the appropriate direction. Short breaks of a few minutes each (1–10 min) were taken between trials.

Scoring

All trials were scored from the videotapes by E1. For purposes of scoring, a trial began when the subject first moved its head to look somewhere other than at E1 (regardless of whether this involved a delay relative to E1's moving of his head to give the gaze cue). The subject's gaze behaviour during the next 5 s was scored in terms of discrete 'looks'. The subject could look in one of three ways.

(1) Look at target: the subject looked towards the top and back of the cage on the side wall furthest from the subject, that is, the general area where E1 looked in the Target only and the Target with distractor conditions.

(2) Look at distractor: the subject looked sideways towards the place where E2 and the distractor object were located in the Distraction only and Target with distractor conditions.

(3) Look at other: the subject looked anywhere other than the Target or Distractor locations.

A subject could look several times within the 5 s. A look was scored if the subject's gaze moved from any one of the three possible locations to any one of the other two possible locations and paused for ca. 1 s or more (shifts in gaze behaviour within a location were not scored). For purposes of statistical analysis, each trial was then classified in its entirety (regardless of how many looks it contained) as containing Looks at target only, Looks at distractor only, Looks at both target and distractor or No looks at target and distractor (i.e. all looks were Looks at other).

To assess interobserver reliability, a randomly selected 36 of the 180 trails (20%) were scored by a second independent observer (approximately equal numbers of trials from each experimental condition). In these trials there were a total of 89 looks. The observers disagreed on the location of seven looks, for a percentage agreement score of 92%.

Results

Each trial for each subject was classified as Target only, Distractor only, or both target and distractor based on where the subject looked (multiple looks to a single location within a trial were ignored, and trials in which the subject looked at neither target nor distractor were not used in the analysis). In trials with no target or no distractor, the subject could still be counted as looking at the target or distractor if it looked to the location where they did appear in other conditions. We then analysed these data in a 3 (Experimental condition: Target only; Distractor only; Target with distractor) × 3 (Subject response: Look to target; Look to distractor; Look to both) ANOVA. In terms of main effects, subjects did not look more in one condition than the others summed across all

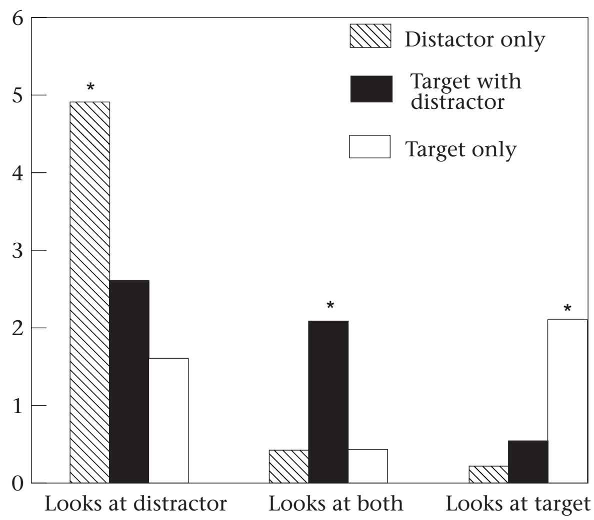

Figure 3. The number of looks at different locations by subjects in the three experimental conditions in experiment 2. (The total possible in each case is 6.) *: Significantly different from each of the other two conditions (P<0.05).

locations, but they did look more at the distractor than at the other two locations summed across all conditions ($F_{2,81}$=36.85, P<0.001). The interaction between experimental condition and subject response was significant ($F_{4,81}$=18.70, P<0.001; Fig. 3), indicating that subjects looked at the different locations differently as a function of experimental condition.

Post hoc, pairwise comparisons (using the Tukey method) revealed the following specific pattern of results underlying the interaction between the two experimental variables (Fig. 3). Subjects looked at the distractor more in the Distractor only condition than in either of the other two experimental conditions (P<0.05 in both cases). They looked at the target more in the Target only condition than in either of the other two experimental conditions (P<0.05 in both cases), and they looked at both the target and the distractor more in the Target with distractor condition than in either of the other two experimental conditions (P<0.05 in both cases). These results indicate that as a group, the subjects looked preferentially at the place where E1 was looking in both the Target only and Distractor only conditions, whereas in the Target with distractor condition they looked quite often at both, indicating that the distractor was indeed salient in this condition but subjects none the less looked at the target as well.

In terms of individual performance, the majority of subjects were consistent with the group results shown in Fig. 3. Specifically, five of 10 subjects looked at the distractor most often in the Distractor only condition, at the target most often in the Target only condition, and at both target and distractor most often in the Target with distractor condition. If ties within a category are allowed (e.g. a subject has equal numbers of looks at target and looks at both in the Target only condition), then seven of 10 subjects fitted the pattern.

Discussion

These results agree very strongly with those of experiment 1 in suggesting that chimpanzees follow gaze direction geometrically. If chimpanzees were working with a low-level model, they would have turned in the direction of E's gaze in all three conditions, stopping at the distractor equally in the Distractor only and Target with distractor conditions; but they did not. When E looked only at the distractor they stopped and looked at it about 10 times more frequently than in the other two experimental conditions. Conversely, when E looked only at the target at the back of the room, subjects looked at the target more than in the other two conditions. When E looked at the target but an interesting distractor was present, the chimpanzees quite often looked both at the target and at the distractor, although they also often looked at the distractor only. This general pattern of results held for over half of the subjects when they were analysed individually. In some ways these findings are stronger than those for human infants, as Butterworth & Jarrett (1991) found that 18-month-old human infants looked past distractors only when the target was still in front of them (or to the side), not when it was behind them as in the present study.

This last finding points out the methodological dilemma of the study. If the distractor was not salient enough, then in the Target with distractor condition chimpanzees would have ignored (looked past) the distractor, and thus made it impossible to infer that they were following E's gaze past a distractor (since there would have been no effective distractor at all). On the other hand, if the distractor was too salient, then the subjects would have stopped at it under all conditions since it was so captivating, and again it would have been impossible to argue that they were following E's gaze past a distractor (since indeed they did not). Luckily, a moderately salient distractor was found fairly easily, and the chimpanzees found it distracting but not inordinately so. If anything, the distractor was a little too distracting, as subjects in the Target with distractor condition quite often stopped at the distractor. The fact that across all conditions subjects looked most frequently at the distractor confirms this interpretation. This makes their tendency to look at both the distractor and the target in the Target with distractor condition, which they did almost exclusively in this experimental condition, all the more impressive since it demonstrates their persistence in locating the target of E's gaze.

GENERAL DISCUSSION

Overall, the results of the two experiments reported here are clear in suggesting that the low-level model of chimpanzee gaze following, namely, that chimpanzees turn in the direction in which the other turns and then look for something interesting on their own, is incorrect. In experiment 1, chimpanzees followed E's gaze direction around four different kinds of barriers, demonstrating much skill in locating the exact terminus of E's gaze. In experiment 2, chimpanzees quite often followed E's gaze direction past a distractor to a location behind them, demonstrating that they would not accept just any object in the general direction of E's gaze, but rather wanted to sight his visual target specifically. More positively, these two results suggest that, like human infants from around 18 months of age (Butterworth & Jarrett 1991), chimpanzees follow the gaze direction of other animate beings geometrically.

It is still not clear from these studies, however, whether and in what ways chimpanzees attribute mental significance to the visual behaviour of others. Thus, when 18-month-old human infants track the visual gaze of others past distractors, Butterworth & Jarrett (1991) do not believe that they understand that the other person is having the mental experience of 'seeing', and a variety of other lines of research on children's social cognition ('theory of mind') confirms that view (Flavell 1997). In addition, although domestic dogs have not been tested in precisely the situations of the current studies, they are quite skilful in following human gaze to opaque containers with food in the context of other distracting containers (Miklósi et al. 1998). Indeed, in one experimental condition of Hare & Tomasello (1999), a human stood close to one container and looked across and over another container to a third container at the far end of the array, and domestic dogs went most often to the third container, ignoring the other two. The relevance of the work with human infants and dogs is simply that if we wish to use the current data to infer that chimpanzees understand the mental event of 'seeing' as others experience it, then we will have to make the same attribution to 18-month-old infants and domestic dogs.

On the other hand, evidence is mounting that chimpanzees do indeed understand the visual behaviour of other animate beings in some fairly sophisticated ways. Call et al. (1998) found that on many occasions when a chimpanzee tracked human gaze to a location and saw nothing as a result, it looked back to the human's face, as if to make sure it had followed correctly, and then followed the gaze direction again. With human infants this behaviour is called 'checking back' (Bates 1979), and it is accorded much significance by some (although not all) researchers in indicating that infants understand that other persons see things. Also, in a recent, unpublished study, B. Hare, J. Call, B. Agnetta & M. Tomasello found that in food competition situations with conspecifics, chimpanzees showed in several ways that they knew what their competitor could and could not see; for example, they seemed to know that some foods were visible to them but not to their competitor (because of the placement of certain barriers). In combination with the present results (and those of Povinelli & Eddy 1996), these findings suggest that chimpanzees do not just follow the gaze direction of others generically, and they do not just learn gaze direction as a simple discriminative (arbitrary) cue; they actually understand something about the visual activities of other animate beings.

One possible hybrid explanation involves a combination of a species-universal tendency to follow the gaze of others and individual learning about the differential significance of gaze in different physical situations. For instance, individual chimpanzees must experience many social situations in which they: (1) notice and follow the gaze direction of a conspecific; (2) see a barrier of some sort; and (3) subsequently see the target of the conspecific's gaze, because the barrier moves, the target moves, or the individual moves around the barrier. The subjects in our study have certainly experienced situations such as these many times because they live with a number of physical barriers, including such things as barrels, walls, concrete conduits through which they locomote, and, perhaps most frequently, conspecifics blocking their view. These individuals have thus had the opportunity to discover the significance of gazing by other individuals in various situations of occlusion, and so one explanation is in effect that chimpanzees use the gaze of others as a social cue and they have learned several variations as to how this cue works in different physical situations. The fact that there were such marked differences in the performance of individuals in our study provides at least some support for this hypothesis. Of the nine individuals who participated in both experiments, two were quite skilful in both tasks (Sheila, Tai), one was poor in both tasks (Magnum) and six were skilful in one task but not the other (four better in experiment 1, two better in experiment 2). Perhaps the different individuals have had different experiences with regard to tracking the gaze of conspecifics around barriers and/or past distractors.

This hybrid explanation, that chimpanzees have a natural tendency to follow usual gaze and they also learn about gaze direction in different situations, is not a simple discrimination learning explanation. Chimpanzees do not just arbitrarily associate gaze direction with outcomes, and indeed in experiment 1 food had no effect on performance. Rather, they come to understand what kinds of conspecific visual activities in what kinds of situations affect behaviour in what kinds of ways. To test this hypothesis, developmental studies of gaze following of chimpanzees at different ontogenetic stages are needed, ideally involving individuals with different but known experiences with barriers and distrators. It would also be important to know if this hybrid explanation also applies to other primate species, for example, those that have demonstrated a general tendency to follow a gaze in experimental situations (Itakura 1996; Tomasello et al. 1998), since the prevalence of this behaviour in different species would also give us valuable information about its possible phylogenetic and ontogenetic mechanisms. In any case, to demonstrate that chimpanzees or other primate species understand the mental significance of the gaze behaviour of other animate beings (in the sense that they understand that the other is actually seeing something comparable to their own experience of seeing), will require additional experimental methods.

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