Five primate species follow the visual gaze of conspecifics

MICHAEL TOMASELLO, JOSEP CALL & BRIAN HARE
Department of Psychology
and
Yerkes Regional Primate Research Center, Emory University

Abstract. Individuals from five primate species were tested experimentally for their ability to follow the visual gaze of conspecifics to an outside object. Subjects were from captive social groups of chimpanzees, Pan troglodytes, sooty mangabeys, Cercocebus atys torquatus, rhesus macaques, Macaca mulatta, stump-tailed macaques, M. arctoides, and pigtail macaques, M. nemestrina. Experimental trials consisted of an experimenter inducing one individual to look at food being displayed, and then observing the reaction of another individual (the subject) that was looking at that individual (not the food). Control trials consisted of an experimenter displaying the food in an identical manner when the subject was alone. Individuals from all species reliably followed the gaze of conspecifics, looking to the food about 80% of the time in experimental trials, compared with about 20% of the time in control trials. Results are discussed in terms of both the proximate mechanisms that might be involved and the adaptive functions that might be served by gaze-following.

The ability to follow the direction of conspecifics' visual gaze would seem to be a social skill with immediate adaptive benefits. Following the gaze of others might help individuals perceive important entities in the environment such as food, predators, and certain kinds of social interactions among group-mates. This social cue might be especially helpful for highly social species, such as many primates, that need constant information about group-mates' activities. A number of field primatologists have made informal observations suggesting that some primate species may follow the gaze of conspecifics: for hamadryas baboons, Papio hamadryas (Kummer 1967); for long-tailed macaques, M acaca fascicularis (de Waal et al. 1976); for savannah baboons, Papio cynocephalus (Byrne & Whiten 1992); and for chimpanzees, Pan troglodytes (Plooij 1978).

The problem is that in each of these cases there may have been some external stimulus that both primate individuals perceived and oriented to and that the human observer did not perceive, raising the possibility that gaze direction was not in fact the effective cue. Menzel (1973, 1974) reported a series of experiments with chimpanzees in which this could not have been the case. In all of these studies, one captive chimpanzee knew the location of food while its group-mates did not. When allowed to search as a group, the group-mates were able to use the behaviour of the knowledgeable individual to determine successfully the food's location. In this situation, however, the knowledgeable individual provided the group-mates with a host of cues to the food's location, perhaps most importantly, direction of travel. There was thus no way in these experiments to know whether gaze direction by itself was responsible for the group-mates' success in finding the food.

The few experimental studies with primates conducted on this issue all have used human experimenters as the animate being whose gaze was being followed. For example, Povinelli & Eddy (1996, study 1) had six 5- to 6-year-old chimpanzees individually enter a room, whereupon they encountered a human experimenter facing them. As soon as the subject had spied her,
the human oriented both her eyes and head to a distinct location, in some cases to the corners of the room above and behind the subject (see also Povinelli & Eddy, in press). In another condition, the experimenter moved only her eyes toward these same locations. In both of these situations, the chimpanzees looked where the human was orienting more than in a baseline condition in which the human looked directly at the subject. This result held even when the chimpanzee encountered the human already looking at a location, thus demonstrating that movement of the head and eyes was not a critical social cue.

In a similar study with a different experimental paradigm, Anderson et al. (1995) found negative results with a pair of capuchin monkeys, Cebus apella. In this study, an experimenter secretly baited one of two food wells and then presented them to the subject. Using several social cues over different trials, direction of eye gaze (including head direction) was not an effective cue in orienting subjects to the hidden food (but touching the baited food well was). Itakura & Anderson (1996) trained a single capuchin monkey to follow human eye gaze to hidden food in a similar situation, but it took them over 120 trials to do so, suggesting the possibility that gaze direction was learned as a straightforward discriminative cue.

In the only study to investigate multiple species within the same paradigm, Itakura (1996) investigated 11 primate species (two species of lemur, two species of cebus monkey, one species of squirrel monkey, four species of macaque, and two species of great ape). For all individuals a human experimenter approached their cage and tried to make eye contact, at which point he then fixed his gaze behind the subject, either to the right or to the left. In some cases, the gaze was accompanied by a pointing gesture. When there was no pointing, only the single orangutan, Pongo pygmaeus (out of 40 subjects total) reliably oriented in the direction of the human's gaze. When there was pointing, the most frequent response from most species was to ignore the experimenter's gaze and pointing. Given that they did respond, however, subjects of 10 of the 12 species followed the gaze and pointing of the human more than they looked in the other direction (the exceptions were the squirrel monkeys and the pigtail macaques). One possible explanation is that the pointing gesture simply caused individuals to look at the hand as it was being extended, and thus to begin orienting in the direction in which the hand was moving, without necessarily understanding the social significance of the pointing or the gaze.

Overall, then, there is inconsistent evidence that non-human primates can follow the gaze of humans to specific locations. The only solid experimental evidence, in the absence of other cues such as pointing or direction of travel, comes from six chimpanzees in one study and a single orangutan in another study, thus suggesting the possibility of ape-monkey differences of social cognition as hypothesized by some primatologists (e.g. de Waal & Luttrel 1988; Byrne & Whiten 1992; but see Tomasello & Call 1994 for a different view). Moreover, there is no experimental evidence, and only scattered anecdotal reports for only a few species, that non-human primates can follow the gaze of conspecifics under any conditions. The purpose of the current study, therefore, was to investigate experimentally the ability of five primate species from three different genera to follow the gaze of conspecifics to a relatively distal object within a relatively natural social setting.

**METHODS**

Subjects were housed in social groups in relatively large enclosures at the Yerkes Regional Primate Research Center Field Station. Enclosures ranged from about 15 × 15 m to about 30 × 30 m. The group sizes were as follows: 15 rhesus macaques, M. macaca mulatta, 38 stump-tailed macaques, M. acaca arctoides, 44 pigtail macaques, M. acaca nemestrina, 18 chimpanzees, P. troglodytes, and 28 sooty mangabeys, Cercocebus atys torquatus. All groups were composed of individuals of both genders; ages ranged from juveniles to adults. No feeding or other caretaking activities were modified for the current study.

Each group was observed by an experimenter from a 6- to 8-m high observation tower overlooking the group’s enclosure (observation distances were approximately 8–30 m). An experimental trial was as follows. The experimenter identified a situation in which two individuals were in proximity to one another, one facing away from the tower (the subject) and one at least partially facing the tower (the conspecific). The experimenter then held up a preferred food item (orange) in an attempt to gain the attention of the conspecific.
The behaviour of the subject was then observed for the next 10 s. Control trials were identical to experimental trials, except that there was no conspecific present in the immediate vicinity of the subject. That is, the experimenter identified an individual subject not facing the tower, held up the food, and observed its behaviour for the next 10 s (Fig. 1). We videotaped all trials of both types from the tower for subsequent analysis.

There were an average of 72.4 trials across species (range=120 trials for the mangabeys and 44 trials for the stumptail macaques). For two species (chimpanzees and stumptail macaques) the experimenter could reliably identify individuals. For chimpanzees, 15 individuals were observed as subjects (two to nine trials per subject); for stumptails, 17 individuals were observed as subjects (one to four trials per subject). In the other species, we took care to sample from as many different individuals as possible; that is, for all species, the experimenter was careful to sample from different individuals across adjacent trials and to sample across various sectors of the compound over time. Comparisons between sectors revealed that for no species was any one sector predominant (for example, in no case were trials taken from the most frequent sector more than twice as frequent as the nearest competitor).

Scoring was conducted by two independent observers viewing the videotapes. For control trials, each observer viewed each trial and determined whether the subject looked to the food within the 10-s window (as in all studies of gaze-following, head direction served as the main operationalization of gaze direction). Because the food was held up directly above the camera, this determination (look, no look) was relatively straightforward. For experimental trials, observers also determined whether the conspecific looked up as it was supposed to and, when it did, whether the subject noticed the conspecific's look (as quality checks on the experimental manipulation). Thus, we categorized trials intended to be experimental as: 'No gaze by conspecific' (the conspecific did not look, so the experimental cue was not available to the subject); 'Gaze not perceived by subject' (the conspecific looked but the subject did not notice, and so the experimental cue was potentially available but not used by the subject); and 'Gaze perceived by subject' (conspecific looked and subject noticed: the only truly experimental trials). For all three of these types of trial, we also recorded the subject's response within the 10-s window (look, no look). The 'No gaze' and the 'Gaze not perceived' trials may be thought of as secondary control conditions, because they are identical to the experimental trials except that, respectively: (1) the conspecific did not provide the gaze cue; or (2) the subject did not perceive the gaze cue given by the conspecific.

Across all species, inter-observer reliability was computed by means of a Cohen's kappa between the two observers (Bakeman & Gottman 1986). Observers agreed whether or not a subject looked on 97% of the control trials, yielding a kappa of 0.89. We categorized each experimental trial into one of four mutually exclusive and exhaustive categories created by crossing the two determinations: experimental versus secondary control (No gaze and Gaze not perceived) and Subject look versus Subject no look. The two observers agreed
on the category for 92% of the experimental trials, yielding a kappa of 0.83.

RESULTS

Subjects in all five species looked at the food significantly more often in the Gaze perceived trials than in the control trials (rhesus: $\chi^2 = 17.8$, $N = 42$, $P < 0.001$; pigtails: $\chi^2 = 16.0$, $N = 54$, $P < 0.001$; stumptails: $\chi^2 = 32.6$, $N = 40$, $P < 0.001$; chimpanzees: $\chi^2 = 15.8$, $N = 56$, $P < 0.001$; mangabeys: $\chi^2 = 30.2$, $N = 88$, $P < 0.001$; Fig. 2). Subjects in all five species also looked at the food significantly more often in the Gaze perceived trials than in either of the secondary control conditions. They looked more in the Gaze perceived trials than in the No gaze trials (rhesus: $\chi^2 = 10.7$, $N = 42$, $P < 0.001$; pigtails: $\chi^2 = 5.4$, $N = 28$, $P < 0.05$; stumptails: $\chi^2 = 34.0$, $N = 34$, $P < 0.001$; chimpanzees: $\chi^2 = 10.0$, $N = 29$, $P < 0.01$; mangabeys: $\chi^2 = 11.1$, $N = 36$, $P < 0.001$). They also looked more in the Gaze perceived trials than in the Gaze not perceived trials (rhesus: $N = 26$, $P < 0.03$, Fisher’s exact test; pigtails: $\chi^2 = 23.4$, $N = 41$, $P < 0.001$; stumptails: $N = 26$, $P < 0.001$, Fisher’s exact test; chimpanzees: $\chi^2 = 15.2$, $N = 36$, $P < 0.001$; mangabeys: $\chi^2 = 16.7$, $N = 50$, $P < 0.001$). None of the three control conditions differed significantly from one another.

In characterizing the behaviour of subjects, latency to respond to the conspecific’s look seemed to be important. Latency to look was thus determined for each trial, with a mean and median value computed for each species. The mean values (in seconds) were: rhesus: 0.92, stumptails: 0.46, mangabeys: 1.68, and chimpanzees: 1.00. The median response time for four of the species was 0 s (i.e. less than 1 s); rhesus had a median value of 0.50. Thus, all species responded almost immediately after spying the gaze cue. Vocalizations almost never occurred in the trials, either from the conspecific or subject. Oranges are a food all five of the subject species like very much, but this fruit did not elicit an extreme response because subjects ate oranges almost daily.

A n argument could be made that the Gaze not perceived trials should be grouped with the experimental trials, because the conspecific looked, and thus provided a potential cue for the subject, even though the subject did not notice this cue as reliably judged by two independent observers. When we grouped subjects in this way, results still
corroborate the previous findings in that subjects in four of the five species still looked at the food significantly more often in the new experimental condition than in the control condition (rhesus: $\chi^2_1=11.7$, $N=52$, $P<0.001$; stumptails: $\chi^2_1=23.2$, $N=44$, $P<0.001$; chimpanzees: $\chi^2_1=5.0$, $N=74$, $P<0.03$; mangabeys: $\chi^2_1=13.3$, $N=120$, $P<0.001$; Fig. 3). Pigtail macaques also showed the same pattern, although these results were not statistically significant ($\chi^2_1=3.3$, $N=72$, $P<0.08$).

Even though subjects looked at the food in the vast majority of the Gaze perceived trials across all species, they did not do so in all trials. We therefore explored the possibility that some behaviour patterns in the conspecific may have facilitated the subjects’ gaze-following. We looked at two behaviour patterns specifically: (1) the presence of a distinctive head movement; and (2) other salient behaviour (for example, head bobbing) that might have attracted the subjects’ attention. We thus noted the presence of these behaviour patterns for each Gaze perceived trial and related this to the outcome of that trial. Neither the conspecific’s head movement nor any other salient behaviour was reliably associated with subjects’ looks to the food ($\chi^2$, $\alpha_S$); all five species showed a similar pattern of results.

**DISCUSSION**

In the current study we found that five primate species from three different genera reliably followed the gaze of conspecifics to external objects over 80% of the time when the conspecific provided a clear gaze cue that was noticed by the subject. Subjects of all five species did this in an experimental setting in which the possibility of their noticing the external objects for themselves was ruled out, as evidenced by the small amount of looking (less than 20% of the time) in the control conditions (control, No gaze, and Gaze not perceived). When subjects did perceive the gaze of conspecifics, they looked in the same direction almost immediately thereafter (less than 1 s).

Although primate field workers have long suspected that primates use the gaze direction of others as a cue to the presence of external entities, the current findings are the first to document this fact experimentally. Our findings further suggest that studies in which primates do not follow the gaze direction of humans (e.g. Itakura 1996) may reflect more of a motivational problem than a competence problem. Primates are much more interested in where conspecifics are looking than in where humans are looking. The main possibility for ambiguity in the current findings is how the
Gaze not perceived trials were treated. But for four of the five species it made no statistical difference whether these trials were included in the experimental trials (and for the other species P <0.08). This finding suggests that not only can primates use gaze direction as a cue when they notice it, they often do use it when it is produced in their immediate vicinity.

We did not attempt to determine precisely what behavioural cues were being used by the subjects in the current study. In particular, we do not know whether individuals used head direction in general, or something more specifically with the eyes. However, body orientation in general could not have been the cue, because in both the No gaze and Gaze not perceived conditions the conspecific was oriented toward the food. We do not know whether the affective state of the conspecific while gazing was a part of the cue, but the conspecifics almost never vocalized (which they often do if highly desirable food is present) and we did not notice many obvious signs of emotional arousal during the looks. Nevertheless, if the conspecifics in this study had spied an object that frightened them, it is possible that the subjects would have noticed a different affective component to their gaze behaviour and behaved differently. Further research is needed to determine whether these additional affective cues are reliably used by primates in their everyday social interactions in which they follow conspecific gaze.

The current results provide no evidence for a difference between monkey and ape social behaviour or cognition. Both monkeys and apes used the gaze direction of conspecifics to locate food, and they did so equally well. This is not surprising from a functional point of view, because there are no differences in the social organization or behaviour of the species of monkeys and apes tested that would lead us to suspect different processes of social behaviour or social cognition (Tomasello & Call 1994, 1997). All of the species in the current study are capable of using something like the ‘attentional structure’ of conspecifics to gather information about external events (Chance 1967).

These results say nothing about how primates understand the significance of conspecifics’ gaze in terms of the attentional or mental states involved. The fact that primates follow the gaze of conspecifics may have either a ‘rich’ interpretation, in terms of primates’ use of social cues in their creation of social and other behavioural strategies (Povinelli & Eddy, in press). Only further research can answer the question of the most appropriate level of interpretation. To be ecologically valid, such research should investigate primates’ understanding of the visual gaze, affective states, and possibly mental states, not of human beings but of conspecifics.

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