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Attending to behaviour versus attending to knowledge: examining monkeys' attribution of mental states

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Abstract. The ability of monkeys to attribute mental states such as ignorance to each other was examined in two experiments using four captive groups of Japanese and rhesus macaques, *Macaca fuscata* and *M. mulatta*. In the first experiment, females were shown food or a predator, either in the presence of their offspring or alone, to determine whether they would attempt to alert ignorant offspring more than knowledgeable ones. The behaviour of mothers appeared to be unaffected by the knowledge of their offspring. In the second experiment, a juvenile offspring of a dominant female was isolated in an enclosure with a normally subordinate adult female while the juvenile's mother sat nearby behind either a glass barrier, an opaque barrier or a one-way mirror. In the mirror condition, the two subjects could see the mother, but she could not see them. The behaviour of subjects under the mirror condition was intermediate between that under the glass and opaque conditions. Subjects were probably sensitive to the mother's orientation and attentiveness, but there was no evidence that they recognized the difference between their own visual perspective and that of the mother.

Monkeys and apes are clearly adept at recognizing the similarities and differences between their own and other individuals' social relationships. What is not known is whether they are equally adept at recognizing the similarities and differences between their own and other individuals' states of mind (e.g. discussions by Premack & Woodruff 1978; Cheney & Seyfarth 1990; Whiten, in press). For example, in many species of monkeys and apes, subordinate males will only attempt to copulate after they have manoeuvred their partners into a position out of sight of more dominant males (for many similar anecdotes see de Waal 1982, 1989; Byrne & Whiten 1988). But what is the basis of this apparent deception? Does a subordinate male copulate behind a bush because he knows that he can influence what the dominant male sees and therefore knows? Or does the subordinate male go behind a bush simply because he has learned from past experience that he can avoid attack whenever he copulates out of sight of the dominant male? There is very little evidence that monkeys ever act to alter the beliefs of other animals, rather than their behaviour. We have no evidence that 'deception' is not simply the result of acutely observed behavioural contingencies derived from past experience: if I do X, he will do Y.

A consideration of alarm calls reveals similarly incomplete evidence for an ability to attribute mental states to others. Alarm calls in many species of birds and mammals are not obligatory but depend on social context. Individuals often fail to give alarm calls when there is no functional advantage to be gained by alerting others; for example, when they are alone or in the presence of unrelated animals (e.g. roosters, *Gallus gallus*: Gyger et al. 1986; ground squirrels, *Spermophilus beldingi*: Sherman 1977; vervet monkeys, *Cercopithecus aethiops*: Cheney & Seyfarth 1985). In all studies to date, however, signallers call regardless of whether or not their audience is already aware of danger. Vervet monkeys, for example, will continue to give alarm calls long after everyone in the group has seen the predator (Cheney & Seyfarth 1981, 1985). There is no evidence that animals recognize that other individuals can possess knowledge different from their own, or that they selectively inform ignorant individuals more than knowledgeable ones.

Like alarm calls, food calls can function to inform others of relevant features of the environment. Even among chimpanzees, *Pan troglodytes*, however, there is no evidence that signallers take into account their audience's state of mind when giving calls. Chimpanzees' loud calls appear to convey precise information about the presence and abundance of food. However, calling rate seems to be influenced primarily by the relative abundance of the resource (Wrangham 1977; see also Hauser &

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Wrangham 1987). Although one experiment conducted with captive subjects has suggested that chimpanzees are capable of recognizing that an individual who has seen an event has different knowledge from one who has not (Povinelli et al. 1989), it is not yet clear whether, under natural conditions, chimpanzees ever alter their calling behaviour depending upon whether or not their audience is ignorant or knowledgeable.

In this paper, we describe two experiments designed to investigate the ability of monkeys to attribute mental states to others and to distinguish between their own knowledge and the knowledge of others. The first experiment examines the issue of informing, and considers whether individuals take into account their audience's state of mind when alerting them to the presence of food or danger. Do signallers recognize ignorance in their audience, and, if so, do they make any special effort to alert ignorant individuals more than knowledgeable ones? The second experiment examines whether the behaviour of monkeys is influenced by their audience's apparent presence, as opposed to their audience's knowledge. Do monkeys only take into account their own visual perspective when monitoring each other, or do they recognize that another individual's perspective, and hence the knowledge derived from it, can differ from their own?

Clearly, we cannot claim to resolve the issue of the attribution of mental states in animals with only two experiments. Instead, our experiments represent a preliminary test of an issue that to date has been considered largely in terms of highly suggestive, but largely inconclusive, anecdotes.

EXPERIMENT I

In captivity, Japanese macaques, *Macaca fuscata*, and rhesus macaques, *Macaca mulatta*, frequently give alarm calls when they see technicians with nets, and they often give a 'coo' call when they are fed preferred foods like fruit (Owren et al., unpublished data). Our aim in the first experiment was to determine whether mothers would utter more calls (or in some other way change their behaviour) when their offspring were ignorant of the presence of food or danger than when they were not. Mothers were isolated from the rest of the group, either in the company of their offspring or alone, and then shown either highly preferred food or a 'predator' in the form of a technician with a net. The offspring were then released, alone, into a part of the enclosure where they were in close proximity to the food or the predator.

If monkeys are sensitive to the mental states of others, that is, if they take the knowledge of their audience into account when alerting others to changes in the environment, mothers should have made more effort to alert their offspring when they were ignorant than when they were already informed. On the other hand, if informants are unaffected by their audience's mental states, the behaviour of the mothers should have been similar regardless of whether their audience had also seen the food or danger. Given the observations that the vocalizations of free-ranging monkeys appear to be unaffected by their audience's state of mind, we predicted that offspring knowledge would have no influence on maternal behaviour.

Methods

Experiments were conducted during 1989 on two groups of rhesus macaques and two groups of Japanese macaques. The groups were housed at the California Primate Research Center in outdoor enclosures constructed from two modified corncribs ('arenas'), each measuring 4·7 m in diameter with a conical roof 4·3 m high. The two arenas were connected by a rectangular intercage unit measuring 4·9 × 3·0 m. A capture chute, mounted lengthwise along the back of the intercage unit, was used to capture and temporarily separate one or more animals from the rest of the group. During the experimental period, the two arenas in each enclosure were visually separated from each other by means of a screen erected on the side of the test arena.

All the animals had lived in social groups since birth. One of the rhesus groups was constituted in 1984, while animals in the three other groups had lived together for over 10 years. Each group included one or two adult males (defined as over 5 years old), three to four multiparous females and five to eight nulliparous females, juveniles and infants.

To accustom the animals to the test procedure for both this experiment and the experiment described below, all adult female subjects were separated from the rest of their group and locked in the chute at least twice before the tests began. Similarly, randomly selected individuals were separated from the rest of the group and locked in the test arena. The behaviour of the subjects during these

Table I. Animals used as subjects in experiment I

	Knowledgeable			Ignorant		
	Group	Mother	Offspring	Group	Mother	Offspring
Food trials	901	BY	BO*	901	CY†	CG†
	901	BA	BL*	902	IY	IO
	902	GA	GY	902	IY	IA
	103	JD	JS*	902	EA	EN
	103	LY†	LN†	103	MT	MY
	104	SY	SO*	103	NE	NK*
	104	SY	SW*	104	RY†	RD†
Predator trials	901	CE	CG	901	CE	CY
	901	BY	BO*	902	IY	IA
	901	BA	BL*	902	GA	GY
	902	IY	IO	103	JD	JS*
	902	EA	EN	103	LY†	LN†
	103	NE	NK*	104	SY	SO*
	104	RY†	RD†	104	SA†	SW†

Groups 901 and 902 were composed of Japanese macaques; groups 103 and 104 were composed of rhesus macaques. All offspring were aged between 2 and 4 years of age except IA and CY, who were 5 years old.
*Males.
†Sibling pair.

pre-test lock-outs did not differ significantly from their behaviour during the trials.

We began each trial by locking all but two members of a given group in one of the arenas. The remaining two animals, a mother and her juvenile offspring, were locked in the chute that connected the two arenas. In the 'knowledgeable' condition, mother and offspring were seated next to each other. Each could see the other and both could see the empty test arena. In one set of trials, both individuals watched a human place a highly preferred food (apple slices) in a food bin in the test arena. In a second set of trials, mothers and offspring were presented with a 'predator' in the form of a technician wearing a surgical mask and brandishing a capture net, who then hid behind a barrier next to the test arena. After observing the food or the predator, the offspring, but not the mother, was released into the test arena.

In the 'ignorant' condition, mother and offspring were also locked in the chute, but the offspring was seated at a distance behind the mother, visually isolated and physically separated from her by a steel partition. Now, only the mother could see the placement of food or the hiding of the predator. After this exposure, the offspring, but not the mother, was once again released into the arena.

The subjects' behaviour and visual orientations were noted by voice into a tape-recorder and later transcribed. All vocalizations given by either mother or offspring were recorded on a separate track of the tape-recorder. In the food trials, observations lasted for 15 min, beginning at the moment when the offspring was released into the test arena. At the end of this period, mother and offspring were reunited with each other and the rest of the group. In the predator trials, observations lasted only 5 min, beginning with the offspring's release. This shorter observation period minimized the obvious distress caused to the animals by the sight of the technician.

In both the food and predator trials, seven mother–offspring pairs were tested in the knowledgeable condition, and seven different pairs in the ignorant condition (Table I). Those mother–offspring pairs that were tested as knowledgeable subjects in the food trial appeared as ignorant subjects in the predator trial, and vice versa. All mothers with offspring aged at least 2 years were used as subjects. In three cases, a sibling pair rather than a mother–offspring pair was used, with the older sibling serving as the potential informant. Since the two species did not differ statistically on any behavioural measure used in this study, results from all trials were combined for the purposes of analysis.

Results

Food trials

If informants were influenced by the knowledge of their audience, mothers should have uttered more calls or in some other respect altered their behaviour when their offspring were ignorant of the food than when their offspring already knew the food was present. The behaviour of the mothers, however, seemed unaffected by their offsprings' knowledge. The seven mothers whose offspring were ignorant showed no difference in their behaviour or calling rate compared with the seven mothers whose offspring were knowledgeable, even when the food was initially introduced. Mothers and offspring did exchange vocalizations at low rates, but there was no difference in calling rate between mothers whose offspring were knowledgeable and those whose offspring were ignorant (one-tailed Mann–Whitney U-test, $N_1=7$, $N_2=7$, $U=22{\cdot}5$, NS). Mothers' calling rate was also unaffected by offspring age or sex. Similarly, ignorant offspring did not call more than knowledgeable ones ($U=21$, NS).

The mothers' apparent failure to communicate information about food to their ignorant offspring had immediate consequences. The mean latency for finding and eating food was significantly shorter for knowledgeable offspring than for ignorant ones ($U=13$, $P<0{\cdot}05$, corrected for ties). The primary factor determining whether an offspring acquired food, therefore, was its own knowledge rather than its mother's.

Predator trials

Although all mothers showed distress at the sight of the technician and struggled to free themselves from the chute, none of them uttered alarm calls. The lack of alarm calls clearly made it more difficult to measure any information transmission from informant to audience. Nevertheless, several measures suggested that mothers did not behave differently when their offspring were ignorant from when they were knowledgeable. For example, mothers of ignorant offspring did not orient themselves toward or look at their offspring more than mothers of knowledgeable offspring ($U=17{\cdot}5$, NS).

Mothers were equally attentive to knowledgeable and ignorant offspring even though the behaviour of the offspring themselves differed significantly depending on whether they knew about the predator. Upon seeing the technician, knowledgeable offspring showed distress by crouching and sitting next to their mothers at the entrance of the chute. After being released, knowledgeable offspring spent significantly more time than ignorant ones sitting within arm's reach of their mothers ($U=9{\cdot}5$, $P<0{\cdot}05$). Parallelling results obtained in the food trials, therefore, the determing factor in the amount of anxiety shown by offspring was their own and not their mothers' knowledge.

Discussion

Although mothers failed to utter alarm calls during the predator trials, specialized vocalizations are by no means the only means by which animals might transmit knowledge to each other. As Menzel's (1971) pioneering experiments on chimpanzees demonstrated, considerable information about the location and nature of hidden objects can be conveyed by the signaller's gaze, orientation and affect. In our experiments, however, mothers did not appear to alert their offspring to the food or danger. Although it is possible that mothers gave their offspring some subtle behavioural cues that were not visible to us, the juveniles' behaviour suggested that any such cues were also not apparent to them. Juveniles obtained food significantly faster when they had already seen the food themselves than when the presence of food was known only to their mothers, and they showed significantly more anxiety when they had seen the technician themselves than when the technician had been seen only by their mothers. These results support observational accounts of free-ranging monkeys in suggesting that signallers do not alter their behaviour or calling rate depending upon their audience's knowledge. While chimpanzees may be capable of recognizing ignorance on the part of their audience (Povinelli et al. 1989), monkeys may not.

Might mothers have failed to alert their offspring because they did not know that their offspring were ignorant? While we cannot answer this question definitively, mothers certainly had ample opportunity to determine whether their offspring were ignorant. Under the ignorant condition, no other animals were in sight when the mothers were exposed to the food or the predator, and their offspring were released from behind a steel barrier. Most important, the offsprings' own behaviour was markedly different when they were ignorant than when they were knowledgeable. The question may, however, be moot. If the mothers were incapable of attributing ignorance to others, they could not, by definition, infer whether or not their offspring had seen the food or the predator.

Clearly, these negative results do not allow us to distinguish between the inability to attribute states of mind to others and the failure of this ability to alter behaviour. It remains possible that monkeys do recognize the difference between their own knowledge and the knowledge of others, but that their behaviour is simply unaffected by this knowledge. Whenever knowledge in another species is defined operationally, through behaviour, there is a danger of concluding that an ability is absent when it is simply not manifested. Negative results are of interest, however, when compared with information transmission in humans. While human cultures vary in their emphasis of active informing and pedagogy (see e.g. Boyd & Richerson 1985), in no culture are these modes of information transmission absent. In contrast, pedagogy has yet to be documented conclusively even among chimpanzees (see Cheney & Seyfarth 1990; Visalberghi & Fragaszy, in press, for reviews). If non-human primates are capable of distinguishing ignorance and false beliefs in others, their apparent failure to act on this knowledge is striking.

EXPERIMENT II

In the wild, monkeys and apes sometimes appear to conceal themselves deliberately behind rocks or trees in such a way that they can see others but others cannot see them. Under these relatively uncontrolled conditions, it is difficult for a human observer to determine whether the animals recognize that there can be a difference between their own visual perspective (and the knowledge gained from what they see) and the visual perspective of others. The aim of the second experiment was to investivate whether a monkey can learn that the orientation of a one-way mirror potentially allows her to monitor animals who, though visible, are unable to see her.

The experimental design closely followed one previously adopted by Keddy Hector et al. (1989) in a study conducted on vervet monkeys. In these experiments, a male was locked in an outdoor arena with an infant while the infant's mother sat in a chute at the entrance of the arena, separated from the male and the infant either by a glass partition, an opaque partition or a one-way mirror that allowed the female to see the male but prevented the male from seeing her. In the glass condition, males behaved affiliatively toward the infants. By contrast, in the opaque and one-way mirror conditions, when the mother appeared to be absent, males were more likely to threaten the infant.

It was impossible to determine whether the males' behaviour toward infants under the three test conditions was altered by their attribution of knowledge to the mothers as opposed simply to the mothers' perceived presence, because in these experiments the two were confounded. The experiment described below attempted to distinguish more explicitly between an individual's apparent presence and her knowledge by reversing the orientation of the one-way mirror, so that animals in the test arena could see the observer sitting in the chute even though the observer could not see them.

Subjects for this experiment were the same adult female and juvenile Japanese and rhesus macaques described in experiment I (Table II). In both of these species, offspring acquire dominance ranks similar to their mothers', and the ranks of younger animals are often dependent on the support of their mothers and other female kin (see e.g. Kawai 1958; Datta 1983). Indeed, a study of Japanese macaques has shown that the juvenile offspring of dominant females may become subordinate to the members of normally low-ranking matrilines if the juveniles are deprived of kin support (Chapais 1988a, b).

Our experiment measured the influence of a dominant mother's apparent presence on the agonistic interactions of her offspring and a normally subordinate older female. The offspring of a high-ranking female was placed in an empty test arena with a subordinate adult female under each of three conditions: when the mother was visible behind a clear glass barrier; when the mother was invisible behind a dark opaque barrier; and when the mother was seated behind a one-way mirror. In this last case, the mother could be seen by her offspring and the subordinate female but she could not see them.

We predicted that under the clear glass condition the subordinate female would behave toward the dominant offspring much as she did under normal group conditions and show little agonistic behaviour. In contrast, we predicted that the subordinate female would show more agonistic behaviour

Table II. Animals used as subjects in experiment II

Group	Observer mother	Rank	Age	Offspring	Age	Subordinate female	Rank	Age
901	CE	1/5	8·5	CG	3·0	BA	3/5	11·5
	BY	4/5	15·0	BB*	3·5	AA	5/5	10·5
902	IY	1/4	13·5	ID	5·0	GA	3/4	12·5
	GA	3/4	12·5	GY	2·0	EA	4/4	16·5
103	SY	1/4	9·0	SO*	3·0	RY	3/4	4·0
	SA†	2/4	5·0	SW†*	2·0	PA	4/4	22·0
104	JD	1/4	8·0	JS*	2·0	NE	4/4	8·0
	MT	2/4‡	8·0	MO	4·0	LY‡	3/4	4·0

Legend as in Table I.
For rank, 2/5 indicates that the female ranked second highest among a group of five females aged at least 4 years.
‡LY began to dominate MT and MO in dyadic interactions during the experimental period.

toward the dominant offspring when the mother was invisible behind the opaque barrier.

There were two possible outcomes to the trials using one-way mirrors. If the subordinate female was influenced solely by her audience's apparent presence, her behaviour under the one-way mirror condition should have been indistinguishable from her behaviour under the glass condition. On the other hand, if the subordinate female was capable of distinguishing between her own visual perspective and the mother's visual perspective, she might have realized that the mother was ignorant of what was occurring even though the mother could be seen. If this were the case, the subordinate female's behaviour under the one-way mirror condition should have been indistinguishable from her behaviour under the opaque condition.

Given the many anecdotal observations suggesting that monkeys do not distinguish easily between their own and other animals' states of mind (see Cheney & Seyfarth 1990; Whiten, in press for reviews), we predicted that the subordinate female's behaviour under the one-way mirror condition would be the same as her behaviour under the glass condition. Only the apparent presence of an audience would affect her behaviour; the audience's state of mind would be irrelevant.

Methods

This experiment required that the monkeys become familiar with the properties of one-way mirrors. Therefore, at least 4 weeks before the trials began, we placed a one-way mirror in each cage, at the entrance of the chute. Each side of the mirror was bordered with differently coloured fluorescent tape to allow animals to distinguish between the opaque and transparent sides more easily. We emphasize that this procedure only gave animals the opportunity to learn that each side of the mirror provided a different visual perspective. If monkeys are incapable of comprehending that their own visual perspective can differ from that of another individual, they will never understand how one-way mirrors work.

At the start of each trial, two technicians herded the animals into the chute and separated the subjects from the other members of the group, who were then released into the other half of the enclosure. The mother observer was then locked in the chute behind one of the three barriers and the test dyad was released into the arena. The three subjects could see only each other, although they remained in auditory contact with the other group members. After 30 min of observation, the observer was also released into the arena and the three animals were observed for a further 15 min. Subjects were then reunited with the rest of the group. All comparisons of rates of behaviour before and after the observer's release are corrected for the difference in observation time.

Each set of subjects was tested under each of the three conditions. To minimize order effects, four sets of animals were tested in the glass condition first and four were tested in the mirror condition first. The opaque condition occurred as the second trial for all eight sets of animals. All trials involving the same individuals were separated by at least 3 days. All possible triadic combinations of two females and one juvenile were used, yielding a sample of eight sets of animals for each of the three test conditions (Table II).

Background data on agonistic interactions were obtained from observations during the previous 2 years (M. Owren & J. Dieter, personal communication). The dominance ranks of adult females were determined on the basis of the direction of approach–retreat interactions, chases and open-mouth threat displays. As in other groups of rhesus and Japanese macaques (see above), offspring acquired ranks similar to their mothers' (Owren et al., unpublished data). We refer to the dominant female in the chute as the 'observer'. The two animals in the outdoor arena are referred to in terms of their relative ranks under normal group conditions. Thus, the offspring of the observer is called the 'dominant' animal even though his or her rank may have been dependent upon the presence of the mother. We refer to the older lower-ranking female as the 'subordinate'.

Although subjects almost never exchanged affinitive interactions during the test period, they did exhibit agonistic behaviour in the form of approach–retreat interactions and threats. An approach–retreat interaction (or supplant) was defined as occurring whenever one animal approached to within 2 m of another and the other animal moved at least 0·5 m away. A threat occurred whenever one animal bit, chased, hit, pushed or gave an open-mouth display at another.

We also measured the relative frequency with which subordinate animals approached and left their dominant companions under the three conditions, using the index derived by Hinde (Hinde & Atkinson 1970). This index is defined as the percentage of approaches due to the subordinate minus the percentage of leavings due to the same animal (and then multiplied by 100), where approaches and leavings are defined in terms of changes in distances of 2 m.

Some trials were more likely than others to be affected by external disturbances, for example, when an animal care vehicle drove nearby. To control for these external disturbances in our analysis, we also compare the behaviour of dominant and subordinate subjects prior to the observer's release with their behaviour after her release under each of the three conditions. Throughout the analysis we use a matched-pairs design to control for individual variation under different test conditions. Unless otherwise noted, all statistical comparisons are based on one-tailed Wilcoxon matched-pairs signed-ranks tests.

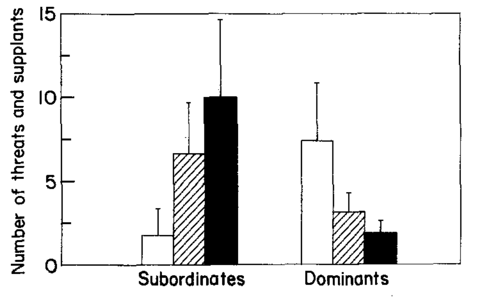

Figure 1. The number of threats and supplants given by subordinate and dominant subjects to their companions under the three test conditions. Histograms show $\bar{X}+\text{SE}$ for eight subordinate and eight dominant subjects. □: glass condition; ▨: mirror condition; ■: opaque condition.

Results

Agonistic behaviour

Before observer's release. As might be expected if the ranks of normally dominant juveniles were to some extent dependent on the support of their older relatives, on average subordinate subjects supplanted and threatened their dominant companions least under the glass condition and most under the opaque condition, with the mirror condition being intermediate between these two extremes (Fig. 1; to increase the sample of agonistic interactions, the analysis combines supplants and threats; results are similar if threats and supplants are considered separately). Significantly more subordinate females showed more agonistic behaviour under the mirror and opaque conditions than under the glass condition (Table III). Although threats were less common than supplants, five subordinate females threatened their dominant companions under the opaque condition, while two did so under the mirror condition and none did so under the glass condition. In two cases (AA and BA), these threats escalated to include hitting and biting, although there were no obvious injuries.

The behaviour of dominant subjects was opposite to that of their subordinate companions. Dominant animals showed most agonistic behaviour under the glass conditions, less under the mirror condition, and least under the opaque condition (Fig. 1). Significantly more dominant subjects were more agonistic under the glass condition than under

Table III. Comparison of the number of subjects who showed more agonistic behaviour under one condition than another

	More agonistic behaviour					
	Glass	Mirror	Opaque	No difference	*T*	*P*
Subordinates						
Glass versus mirror	1	4	—	3	1·5	<0·06
Glass versus opaque	0	—	5	3	0	<0·05
Mirror versus opaque	—	0	4	4	2	>0·15
Dominants						
Glass versus mirror	5	0	—	3	0	<0·05
Glass versus opaque	6	—	1	1	2	<0·05
Mirror versus opaque	—	4	2	2	6	>0·15

All statistical comparisons are one-tailed Wilcoxon matched-pairs signed-ranks tests.

either the mirror or opaque condition (Table III). When threats are considered alone, dominant animals were most aggressive under the glass condition, although in no case did their threats escalate to hitting or biting. It seems possible that their ranks were sufficiently dependent upon the observer that both the observer's apparent absence (under the opaque condition) and her apparent lack of attentiveness (under the mirror condition) affected their agonistic behaviour.

After observer's release. To control for variation in the subjects' behaviour from one day to the next, we also compared subjects' behaviour before the observer's release with their behaviour after her release under the three conditions. If the subjects' agonistic interactions were influenced by the visibility of the observer, we would predict little difference in behaviour before and after release under the glass condition and a substantial difference under the opaque condition. The subjects' behaviour under the mirror condition should have been similar to that under the glass condition if the monkeys failed to recognize that the observer could not see them. If, however, the monkeys were sensitive to the distinction between the observer's physical presence and her knowledge or attentiveness, their behaviour under the mirror condition should have been similar to that under the opaque condition.

As predicted, under the glass condition there was no difference in the agonistic behaviour of subordinates before and after the observer's release (Fig. 2; corrected for ties, $N=2$, $T=0$). In contrast, under both the mirror and the opaque conditions, there was a considerable decrease in the agonistic behaviour of subordinates following the observer's release (mirror: $N=4$, $T=0$, $P<0{\cdot}05$; opaque: $N=6$, $T=0$, $P<0{\cdot}05$).

Dominant animals showed little change in their agonistic behaviour after their mothers' release

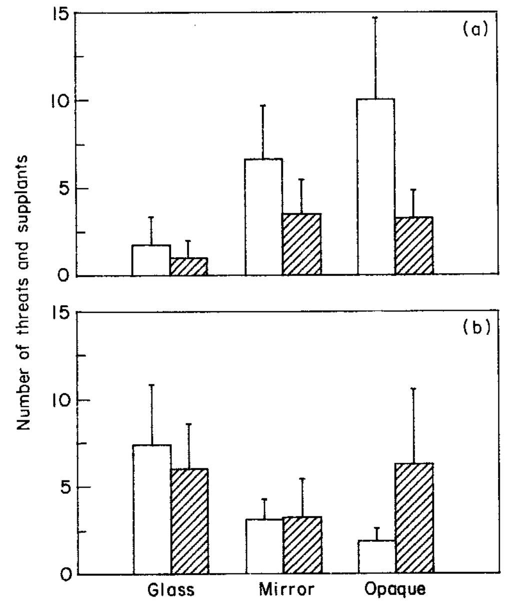

Figure 2. The number of threats and supplants given by subordinate (a) and dominant (b) subjects to their companions before and after the observer's release under the three test conditions. Histograms show $\bar{X}$+SE for eight subordinate and eight dominant subjects. □: period before observer's release; ▨: period after observer's release.

under either the glass ($N=7$, $T=9$, NS) or the mirror condition ($N=5$, $T=6$, NS; Fig. 2). Under the opaque condition, the mean number of supplants and threats given by dominants was higher after the observer's release than before, although this difference was not significant ($N=7$, $T=11$, NS).

The observers' behaviour following release also differed under the three conditions, although in no case were these differences significant. Observers showed slightly less agonistic behaviour under the glass condition, when they had been able to watch the subjects' interactions and when subordinates had been least aggressive, than under either the mirror or opaque conditions, when they had been unable to observe the subjects. The dominant subjects' behaviour following the observers' release never seemed to alert the observers to what had transpired earlier. Dominant subjects never threatened or attempted to recruit the observers' aid following their reunion with the observer, even when they had been threatened or bitten prior to the observer's release.

Access to food

Before observer's release. To determine the effect of separation on access to preferred resources, subjects were fed apple slices both prior to the observer's release and after reunification with her. The amount of food obtained by subordinate subjects under the three conditions provides some measure of the influence of the observer's visibility, attentiveness and perhaps knowledge on the subjects' behaviour. Under the glass condition, five dominant subjects obtained more food than their subordinate companions, and three subordinates obtained more. In contrast, under the mirror condition, all eight subordinates obtained more than dominant animals (one-tailed sign test, $P<0.01$). Under the opaque condition, six subordinates obtained more, and two dominants obtained more.

After observer's release. Not surprisingly, observers almost always excluded subordinate subjects from food following their release. Subordinates were able to obtain food only when the observers did not attempt to approach the food themselves. Under the glass condition, five subjects obtained less food following the observer's release than before, while three obtained none at either time (sign test, $P<0.05$). Under both the mirror and opaque conditions, seven of eight subordinates

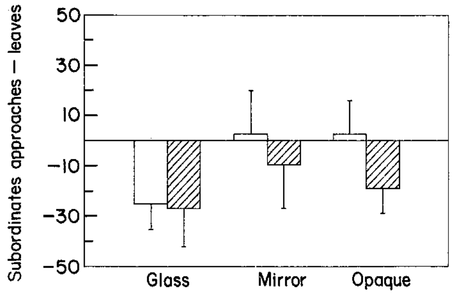

Figure 3. Approach–retreat indices for subordinate subjects relative to their dominant companions before and after the observer's release under the three test conditions. Histograms show $\bar{X}+$SE for eight subordinate subjects. □: period before observer's release; ▨: period after observer's release.

obtained less food following the observer's release (sign test, $P<0.05$).

Approach–leave index for subordinates approaching dominants

Before observer's release. The approach–leave index provides a measure of the relative role of subordinate subjects in maintaining proximity with their dominant companions. A negative figure indicates that the subordinate subject left her companion more than she approached her; the magnitude of this figure therefore provides some indication of the extent to which subordinate females avoided dominant animals under the three test conditions.

As might be predicted if the observer's visibility had some influence on the subjects' relative ranks, a significant number of subordinate subjects had a more negative approach–leave index under the glass condition than under either the mirror or the opaque condition (Fig. 3; Table IV). In contrast, under both the mirror and opaque conditions, the subordinates' indices were slightly positive, suggesting that the subjects behaved as if the observer was not present.

After observer's release. As predicted, there was little difference between the behaviour of subordinates before and after the observer's release under the glass condition; in each case, subordinates had, on average, high negative scores (Fig. 3; $N=7$, $T=11$, NS). By contrast, under both the mirror and the opaque conditions there was an overall change in subordinates' behaviour, with the index becoming more negative following the observer's

Table IV. Comparison of the number of subordinate subjects who had a more negative approach–leave index under one condition than another

	Leave more				
	Glass	Mirror	Opaque	T	P
Glass versus mirror	6	2	—	5	<0.05
Glass versus opaque	7	—	1	2	<0.05
Mirror versus opaque	—	5	3	13	>0.15

'Leave more: glass' indicates that a subject left more (or approached less) under the glass condition than under the mirror or opaque condition. Legend as in Table III.

release (Fig. 3). Under neither condition, however, was this change significant (mirror: $N=8$, $T=8$; opaque: $N=8$, $T=12$).

Other behaviour

Dominant juveniles, subordinate females and observers uttered at least some vocalizations in almost all trials, primarily in the form of coo calls. There was no difference, however, in the number of vocalizations initiated by subjects under the three conditions. Dominant subjects and their observer mothers did not exchange more vocalizations when they were visible to each other than when they were not, nor did subordinate subjects call more under one condition than another.

Similarly, under all three test conditions dominant and subordinate subjects spent at least some time sitting within 2 m of each other. There was no tendency, however, for subjects to spend more time near each other under one condition than another.

Discussion

The results of the trials using glass and opaque barriers support many previous studies in suggesting that the dominance ranks of juveniles are at least to some extent dependent upon the presence of kin. Juvenile subjects were supplanted and threatened significantly more by normally subordinate females when their close kin were hidden behind the opaque barrier than when their close relatives were visible. Subordinate females also approached their dominant companions more (or moved off from them less), and obtained significantly more food. Conversely, dominant juveniles showed more agonistic behaviour when their relatives were visible than when they were not. Both dominant and subordinate subjects also showed more changes in their behaviour following the observers' release from the opaque barrier than from the glass barrier, further suggesting that their behaviour was strongly influenced by the observers' visibility.

On average, results from the mirror trials were intermediate between those from the glass and opaque trials, although more subjects treated the mirrors as if they were opaque than as if they were glass. Significantly more dominant subjects showed agonistic behaviour under the glass condition than under either the mirror or opaque condition. In contrast, significantly more subordinate subjects showed agonistic behaviour under the mirror and opaque conditions than under the glass condition. Similarly, subordinate subjects were more likely to avoid their dominant companions under the glass condition than under either the mirror or opaque condition. Finally, more subordinate subjects obtained food under the mirror and opaque conditions than under the glass condition. When the behaviour of subjects before and after the observer's release was compared, results from the mirror trials again fell between those from the glass and opaque trials, with subordinate subjects showing more changes in their behaviour following the observer's release under the mirror and opaque conditions than under the glass condition.

In summary, subjects treated the mirror barriers less like glass barriers than we had predicted. In some respects, therefore, the monkeys behaved as if they could distinguish between the observer's presence and her knowledge. However, we cannot conclude that the monkeys might have been capable of attributing ignorance to the observers, and of recognizing that the observers' visual perspective was different from their own because we were unable to rule out the more conservative and likely hypothesis that subjects were simply adept at monitoring the observer's behaviour and apparent attentiveness. Under the mirror condition, observers probably did not orient themselves as much toward the arena, and they may therefore have appeared not to be watching their offspring. Rather than recognizing a mental state, the observer's ignorance, subjects may instead have been sensitive to her actions, orientation and the direction of her gaze.

Numerous anecdotes from field observations provide similarly inconclusive evidence for the attribution of mental states by monkeys. When subordinate males copulate from behind bushes, or when females groom subordinate males only after they have first concealed themselves behind rocks (e.g. Kummer 1982), it is impossible to determine whether the animals understand that the spatial perspective and visual field of others differ from their own. Humans as young as 3 years old seem capable of recognizing the distinction between their own physical orientation and the orientation of others (Donaldson 1978; Flavell et al. 1978). Whether monkeys or even apes are also capable of such judgments, however, has not yet been demonstrated conclusively. Animals may simply learn that they can avoid attack if they conceal their actions from more dominant individuals.

It is, of course, by no means a trivial feat to adjust one's own behaviour according to subtle variations in other individuals' orientation and direction of gaze. The ability certainly demands that monkeys recognize that attentiveness can strongly affect actions. It remains to be determined whether they recognize that attentiveness can also affect knowledge.

The experiments described here support what many observational studies have suggested: that monkeys are sensitive to the composition of their audience and that they are astute observers of each other's behaviour and apparent attentiveness. They may be less astute observers of each other's minds.

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