Rhesus monkeys, *Macaca mulatta*, know what others can and cannot hear

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Animals from numerous taxa use auditory information to functionally deceive other individuals, either by producing or withholding various vocal signals. However, little empirical evidence has demonstrated that any nonhuman species recognizes how manipulating auditory information can alter the knowledge state of other individuals. We explored whether one monkey species, the rhesus macaque, understands the connection between hearing and knowing. Monkeys were presented with the opportunity to take grapes from a human competitor who was looking away. One of two grapes was placed inside a silent container, and the other was placed inside a noisy container. We predicted that subjects would selectively choose the silent container over the noisy container, because the noisy container might alert the human competitor to the subject's actions. As predicted, subjects reliably took the grape from inside the silent container when the competitor was not looking. In contrast, subjects chose randomly when the competitor was looking and therefore already knew about the subject's approach. These results demonstrate that monkeys preferentially attempted to obtain food silently only in conditions in which silence was relevant to obtaining food undetected.

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Deception is widespread in the animal kingdom. Even a quick glance at an introductory textbook on animal behaviour will reveal that a variety of nonhuman species behave in ways that serve to confuse and mislead other individuals. For example, in the domain of vocal communication, researchers have long observed that animals from many taxa occasionally use vocal signals in ways that misrepresent information about their environment or emotional state (see Whiten & Byrne 1988; Hauser 1996). Male domestic chickens, *Gallus gallus*, for instance, regularly produce food-associated calls even when no food is available (Gyger & Marler 1988); such deceptive food calling benefits the caller by attracting potential female mates to the area. Similarly, free-ranging rhesus monkeys alter their food-calling rates depending on who is around, sometimes choosing to withhold vocal signals about the presence of high-quality food in order to consume more of the food themselves (Hauser 1992; Hauser & Marler 1993a, b).

Although there is little doubt that animals behave in ways that deceive others, there is still much controversy concerning the cognitive mechanisms that give rise to these deceptive behaviours (e.g. Mitchell 1986; Byrne & Whiten 1988; Whiten & Byrne 1988). At the simplest level, animal deceivers may understand little about how their dishonest behaviours affect other individuals; animals may simply luck into using successfully deceptive behaviours through chance and past reinforcement. Under this 'strategic deception' account (Whiten & Byrne 1998), monkeys may choose to withhold food calls in the presence of high-quality food because doing so by chance in the past led to reinforcing consequences (e.g. having more food to eat). Alternatively, animals may have more flexibility in the deployment of their deceptive behaviours. Under this second, 'tactical deception', account, a potential monkey caller encountering a pile of food might flexibly decide how best to proceed; such a tactically deceptive monkey may have some understanding of how his deceptive actions affect the behaviour of other individuals (e.g. whether they are likely to approach, etc.).

At the most extreme third level, however, animals could reason about their deceptive actions in much the same way as humans do; they may realize that other individuals have knowledge and beliefs and may produce deceptive behaviours with the intention of changing these knowledge states or beliefs (see Dennett 1983; Mitchell 1986;

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Whiten & Byrne 1988). This more complex account of animal deception ('intentional deception') involves a cognitive capacity that psychologists refer to as a theory of mind (ToM), an understanding that other individuals have mental states such as beliefs, knowledge and intentions (see Premack & Woodruff 1978; Heyes 1998; Tomasello et al. 2003). Monkeys capable of using intentional deception would choose to withhold food calls because they would recognize that hearing a food call in the distance will lead others to know about the presence of food. Monkeys therefore withhold food calls because they intend to leave other individuals with inaccurate knowledge about the presence of food to prevent these other individuals from approaching the food.

Historically, there has been little reason to argue that animals ever achieve the cognitive sophistication required for intentional deception. Nonhuman primates, the most widely studied group of nonhuman subjects, have notoriously failed to reason about the minds of others in a variety of empirical tasks (reviews in Tomasello & Call 1997; Heyes 1998; Povinelli 2000). Chimpanzees, *Pan troglodytes*, for example, have consistently failed to take into account what human experimenters can see when asking for food (Povinelli & Eddy 1996) and have neglected to use communicative information about another individual's direction of gaze when searching for hidden food (Itakura et al. 1999; Povinelli et al. 1999; Call et al. 2000). Such failures have traditionally led researchers to conclude that nonhuman primates lack the cognitive machinery necessary for reasoning about the minds of others, and thus, that they also lack the capacity for intentional deception (e.g. Tomasello & Call 1997).

Over the past few years, however, primate researchers have devised several new methodologies to explore what nonhuman primates know about the minds of others (see Hare et al. 2000, 2001; see review in Tomasello et al. 2003). These methods were based on the insight that primates are most likely to show ToM-like abilities in ecologically valid contexts involving competition for scarce resources (Humphrey 1976; Byrne & Whiten 1988; Hare 2001). Using this insight, researchers designed a series of studies examining what chimpanzees understood about the minds of their competitors. Subordinate chimpanzees were pitted against more dominant individuals in contests over pieces of food. Subordinate chimpanzees selectively tried to obtain foods that dominant individuals could not see (Hare et al. 2000; see also Hirata & Matsuzawa 2001) or did not know about (Hare et al. 2001). Recent work suggests that these capacities may not be unique to chimpanzees; rhesus monkeys also chose to take food from human competitors who could not see them, either because the humans' eyes were facing away or because their faces were blocked by an opaque barrier (Flombaum & Santos 2005).

Taken together, these results suggest that primates may have the capacity to reason about the knowledge and perceptions of others. Moreover, they raise the possibility that primates may also have the capacity for intentional deception (i.e. they may selectively present and withhold information with the intent of changing others' perceptions or knowledge). However, much of the recent work on primate ToM abilities has focused on competitive tasks that involve vision (i.e. how seeing leads to knowing and believing). Such modality specificity in these new ToM tasks is unfortunate from the perspective of learning about the nature of deception, because some of the most well-documented examples of primate deception involve the auditory domain (e.g. Hauser 1996).

We attempted to address this problem by examining whether one primate species, the rhesus monkey, recognizes that hearing an auditory signal leads to knowing about it. We tested a free-ranging population of monkeys on the island of Cayo Santiago using a series of competitive approach measures. We chose this population of rhesus monkeys as our behavioural subjects for three reasons. First, we and others have successfully tested subjects with similar approach measures in a number of previous studies (e.g. Hauser et al. 2000; Hauser 2001; Santos et al. 2001, 2002; Sulkowski & Hauser 2001; Flombaum et al. 2004; Santos 2004). Second, there is recent evidence that monkeys in this population recognize the connection between seeing and knowing in at least some competitive situations (Flombaum & Santos 2005). Finally, as described above, rhesus monkeys in this population are known to alter their vocal signals in a way that misleads others (Hauser 1992; Hauser & Marler 1993a, b). Consequently, examining what this population understands about the connection between hearing and knowing may lead to insight into the nature of the cognitive capacities underlying deceptive food-calling behaviour in this species.

EXPERIMENT 1

Method

Subjects

We tested free-ranging rhesus monkeys from the Cayo Santiago population (see Rawlins & Kessler 1987). The Cayo Santiago macaques have been subjects in experiments since the 1930s, and thus are well habituated to human experimenters. Monkeys in this population can be easily identified through ear notches and chest tattoos. Monkeys are provisioned with chow at a number of locations and also forage for foods naturally available on the island (e.g. coconuts, leaves, soil). Monkeys also have occasional access to the foods that human experimenters bring to the island (Santos et al. 2001) and occasionally try to take such foods from the experimenters (Flombaum & Santos 2005).

We tested 27 adult rhesus monkeys; other monkeys were approached by the experimenters but did not complete testing because of interference from other monkeys ($N = 22$), disinterest or departure during presentation ($N = 28$), approach before the presentation's completion ($N = 10$), previous testing ($N = 1$), or experimenter error ($N = 3$).

Apparatus

As in previous studies (Flombaum & Santos 2005), we used purple grapes as a food reward. Grapes were hidden inside two translucent containers made of clear plastic, measuring 15×14 cm at the base, and 10 cm high. Each container had a hinged lid that could be opened to gain

access to the contents of the container. We covered each lid with 20 small gilt brass jingle bells (12 mm diameter) using thin metal wire (Fig. 1). Each container had eight bells on the outside surface of the lid and 12 bells on the inside surface. The first container, the noisy container, had unaltered jingle bells that rang when the container was moved. The second container, the silent container, had bells with their ringers removed, such that moving the container produced no ringing noise. Thus, the noisy and silent containers were visually identical, but were distinguishable auditorily in that the noisy container made a loud jingling sound whenever it was moved while the silent container remained noiseless.

Procedure

The present study uses an approach paradigm, one that capitalizes on the Cayo Santiago macaques' natural interest in the foods that they see human experimenters eating. Although individuals at this field site are provisioned with monkey chow, they are quite curious about the novel foods that they see human experimenters consuming while on the island (see Santos et al. 2001) and often attempt to approach human experimenters to obtain these novel foods (see Flombaum & Santos 2005). However, the monkeys in this population are also apprehensive of getting too close to humans, suggesting that they view humans as potentially dangerous competitors. We therefore reasoned that monkeys should be motivated to take human food only when they can do so without being detected. Thus, we examined whether rhesus monkeys take into account whether a human experimenter can hear them when attempting to take food.

Each subject received only one session involving a single experimental trial. Two experimenters performed the experiment. The first acted as the cameraperson, recording the

Figure 1. A photograph of the human competitor sitting with the two containers used as stimuli. Note that the two containers were visually identical; they were distinguished only in that one made a sound when moved and the other did not.

entire session on a digital video camera. The second experimenter served as the competitor, manipulating the containers and the food. The cameraperson (who was always blind to the condition about to be performed) chose subjects opportunistically, selecting animals that were seated away from other monkeys in a clear area. The competitor then approached the subject from the front and completed the presentation from approximately 2 m away from the subject. The cameraperson followed the competitor and filmed the presentation and the subsequent actions of the subject from a distance of approximately 5 m away from the subject. The cameraperson stood on an extended line connecting the competitor and the subject, so as not to introduce a side bias into the subject's choice (Fig. 2).

On the cameraperson's cue, the competitor began by opening the lid of the container to his left, removing the grape inside and displaying it clearly to the subject. Making sure that the subject was watching, he then returned the grape inside the container and closed the lid. For the duration of the time that the lid was open, the competitor shook the container to display its auditory properties. The competitor then repeated this procedure with the container on his right. The position (left or right) of the noisy and silent containers was counterbalanced across sessions. Once the competitor had completed demonstrating the containers' auditory properties, he moved the container to his left away from his body at approximately a 45° angle, while shaking it. He then repeated this procedure with the container on his right. The competitor then stood up, stared at the subject, walked back approximately 2 m from the containers, squatted down and placed his head between his knees, facing the ground. From this position, the competitor could not see the subject or the containers, but could easily look up from this position at any moment. Subjects were then allowed 1 min to approach and visibly touch one container, at which point the cameraperson ended the session. A subject's choice was thus coded as the first container touched within 1 min. Any subject who failed to touch either of the containers in 1 min or who failed to approach the containers was coded as a 'no approach'.

Coding

Two coding measures were taken. The first was performed online during the experiment by the cameraperson. The second was taken from videotapes acquired on a laptop using QuickTime software (Apple Computer, Inc., San Francisco, California, U.S.A.). These digital videos were then scored by an experimenter who was blind to both the experimental condition (i.e. the audio was off so there was no auditory information) and the experimental hypothesis. Agreement across coders was high (97% of trials).

Results

Of the 27 subjects tested, 14 approached one of the two containers; the others were coded as 'no approaches'. Twelve of the 14 subjects (86%) that did approach chose the silent container over the noisy container (binomial test: $P = 0.006$; Fig. 3).
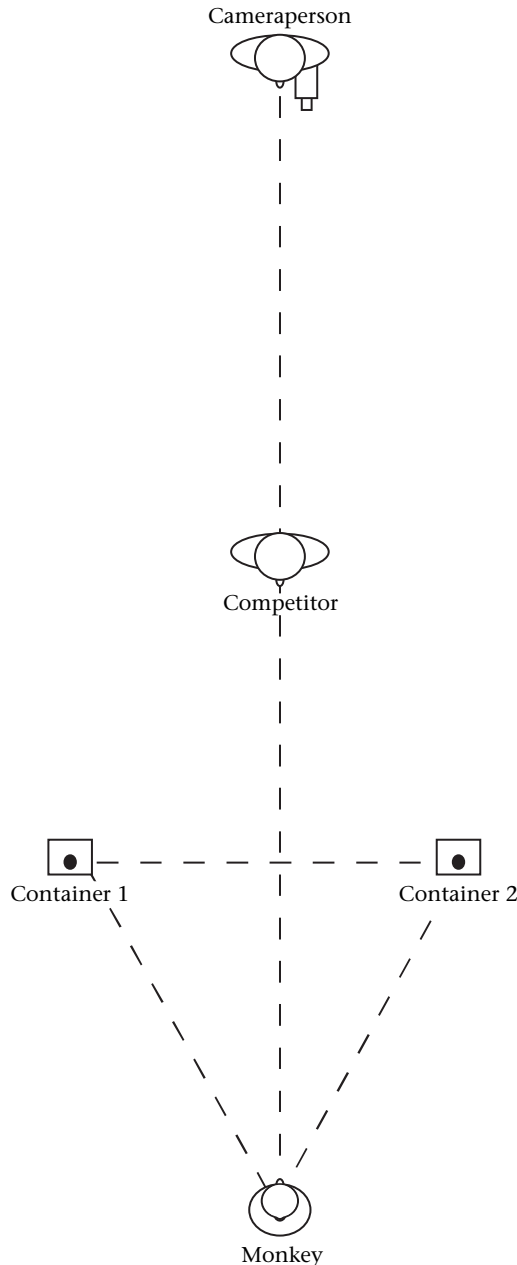
Figure 2. A diagram of the test set-up. The competitor sat approximately 2 m in front of the subject with the cameraperson filming from 5 m behind.

Figure 3. Number of subjects that approached silent and noisy containers across experiments 1 and 2.

Discussion

When given a choice between two containers from which to take a desired grape, rhesus monkeys reliably chose the silent container over the noisy one. Thus, subjects reliably picked the container that did not alert the experimenter to the fact that the grape was being removed. This result suggests that monkeys may take into account how auditory information can change what the experimenter knows. This result fits with previous results from this population (Flombaum & Santos 2005), suggesting that monkeys take into account what a human competitor can and cannot see; in the present experiment,
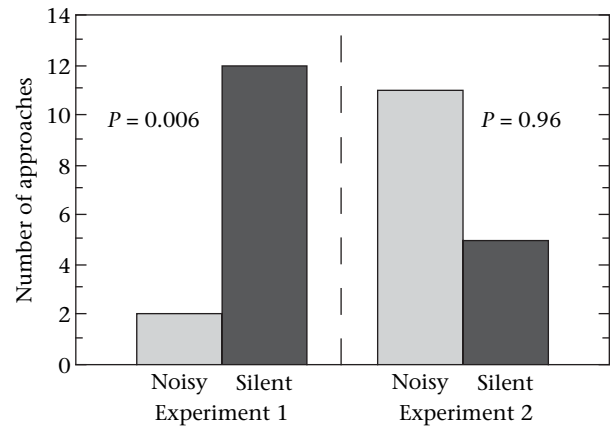
however, monkeys seemed to take into account what a human competitor could and could not hear, selectively approaching in ways that the competitor could not hear.

There is, however, at least one alternative explanation of the results of experiment 1. Subjects may have avoided the noisy container not because they understood the connection between the jingling noise and the competitor's knowledge state, but instead because they were more afraid of the noisy container than the silent one. This account would contend that the presence and position of the competitor did not affect subjects' patterns of approach; they simply avoided the noisy container regardless of how the competitor behaved and without attention to what he could and could not hear during the approach.

To explore this explanation, we ran a second experiment in which the sound produced by the containers no longer mattered to the competitor's knowledge state. More specifically, we presented subjects with the opportunity to take a grape from one of the two containers while the competitor was still looking at the subject, rather than looking away as he had in experiment 1. If subjects avoided the noisy container in experiment 1 because they were afraid of the sound, then they should show this pattern again in experiment 2. In contrast, if monkeys recognized the connection between hearing and knowing, then they should realize that hearing the container move matters only when the competitor does not already know of their plan to approach. For this reason, we predicted that subjects would show a different pattern of approach in experiment 2 than they did in experiment 1 (i.e. they would no longer avoid the noisy container when the experimenter was watching them approach).

EXPERIMENT 2

Method

Subjects

We tested 21 adult rhesus monkeys; other monkeys were approached by the experimenters but did not complete testing because of interference from other monkeys ($N = 33$), disinterest or departure during

presentation ($N = 47$), approach before the presentation's completion ($N = 9$), previous testing ($N = 4$), or experimenter error ($N = 3$).

Apparatus and procedure

The design of experiment 2 was identical to that of experiment 1 except for one change. Once the competitor had completed his auditory demonstration, he retreated approximately 2 m from the containers, squatted down, and continued to look in the direction of the subject. Subjects were again allowed 1 min to approach and visibly touch one container, at which point the session was ended by the cameraperson.

Results

Of the 21 subjects tested, 16 approached one of the two containers; the others were coded as 'no approaches'. Only five of the 16 subjects (31%) that did approach chose the silent container over the noisy container (binomial test: $P = 0.96$). Comparing this pattern of performance to that of experiment 1, subjects preferred the silent container in experiment 1 but not in experiment 2 (chi-square test: $\chi^2_1 = 9.02$, $P < 0.01$; Fig. 3).

Discussion

In contrast to performance in experiment 1, subjects showed no reliable pattern of approach in experiment 2. Just over half of subjects in experiment 2 approached the noisy container when the competitor was looking. This result suggests that subjects' pattern of approach in experiment 1 was not because of either a general preference for the silent container or an aversion to the noisy container. Instead, monkeys seemed to prefer the silent container only when the experimenter was not looking and, therefore, did not know of their approach. Thus, monkeys seemed to take into account the noise caused by their approach only when that noise could change what the experimenter knew about their position and actions.

GENERAL DISCUSSION

The broad aim of the present work was to better explore the proximate mechanisms that could give rise to functional deception in primates. Our more specific aim was to determine whether primates have one of the cognitive capacities required for intentional deception, that is, the ability to recognize the relationship between a deceptive act and its effect on another individual's mental states. We examined whether rhesus monkeys understood the effect of their behaviours on what a human competitor could and could not hear. We presented our subjects with the opportunity to try to take a grape from one of two containers sitting in front of a human competitor. The two containers differed only in one respect, the degree to which they generated noise when moved.

When the human competitor was looking away, monkeys reliably attempted to take the grape from the silent container over the noisy one. Monkeys selectively chose the container that the uninformed competitor could not hear being moved and thus did not know was being moved. In contrast, when the competitor was already watching the monkeys' approach (and therefore already knew of their attempt to take one of the grapes), monkeys chose randomly between the noisy and silent containers. Thus, monkeys chose to obtain food silently only in situations in which silence was relevant to keeping the competitor unaware of their behaviour (i.e. when the competitor could not see that they were approaching).

We interpret these results as evidence that rhesus monkeys may understand how some aspects of their actions (i.e. the noise generated by their approach) can affect the perceptions of other individuals, what they can and cannot hear. The monkeys also seemed to recognize the particular cases in which affecting what others can hear would be to their advantage; monkeys discriminated between situations in which the competitor was and was not looking and therefore those in which he either already did or did not know of their approach. Finally, in addition to understanding the connection between their actions and others' knowledge and perceptions, the monkeys also seemed to be able to act on the basis of that understanding, avoiding the noisy container only in those cases in which its audible movement could inform the competitor of the monkeys' actions.

The results of experiments 1 and 2 corroborate a previous report that monkeys from this population correctly reason about the perceptions of others. Flombaum & Santos (2005) found that monkeys reasoned correctly about what an experimenter could see, selectively taking food from a competitor who was looking away over one who was looking forward. The present findings build on this work in two ways. First, our findings show that rhesus monkeys can reason about another unobservable perceptual state, hearing. Monkeys spontaneously distinguished between actions that a human competitor could and could not hear, selectively acting in ways that the competitor could not hear. Second, our findings suggest that monkeys can spontaneously put information about what a competitor can hear together with information about what that competitor can see, and then act successfully on the basis of what a competitor either does or does not know. Our subjects did not always act on the basis of what the competitor could hear; they did so only when that competitor could not see what was going on. Our results therefore support the idea that monkeys not only recognize the difference between seeing and not seeing, but also seem to reason about how seeing affects the relevance of hearing and not hearing. Our subjects seemed to understand that the competitor's ability to hear their approach was irrelevant if he had already seen (and therefore already knew) that they were approaching. These results provide one of the first demonstrations that non-human animals read mentalistic information from two perceptual modalities and put it together in this way (but see Melis et al., in press, for recent evidence using a similar auditory task in chimpanzee.

Rhesus monkeys' capacity to link information about hearing and seeing has important implications for one of

the theories of nonhuman primates' successful performance in these kinds of mind-reading tasks. Although we (Flombaum & Santos 2005; Santos et al., in press) and others (Tomasello et al. 2003) interpret primates' successful performance in mind-reading tasks as evidence for some form of theory of mind abilities, other researchers have suggested alternative explanations of this performance. Povinelli and colleagues (Povinelli 2000, 2004; Povinelli & Bering 2002; Povinelli & Vonk 2003, 2004), for example, have argued that primates' successful performance in theory of mind tasks can be explained not as mind reading per se, but instead as a sophisticated form of behaviour reading. Under their view, monkeys perform well in mind-reading tasks because they are adept at calculating the statistical likelihood that their actions will lead to specific future behaviours on the part of other individuals; monkeys might recognize, for example, that approaching a competitor who is looking at them is statistically more likely to lead to retaliation than is approaching a competitor who is not looking. In this way, monkeys could succeed in mind-reading tasks by reading and abstracting competitors' behaviours without any knowledge of their mental states.

The present results pose some problems for a behaviour-reading explanation of primate mind-reading successes. Any behaviour-reading account relies on primates having a historic link between some aspect of a competitor's observable features (e.g. the direction that their eyes are pointing) and his future actions (e.g. his likely approach behaviour). Our task, however, used a behavioural methodology that did not involve this historical link. In our task, monkeys must reason about how hearing a jingle-bell sound will affect a human competitors' future pattern of approach. Subjects in this population had no past experience either hearing or making jingle-bell noises until they were used in this study. Moreover, subjects have also had no experience with how a human competitor behaves towards them when they are not looking and a jingle bell is heard. Because monkeys in this population have never had the possibility to test how jingling sounds affect a human competitor's future actions, they could not have built up the experiences needed to make behavioural predictions about the competitor's likely response, which would be required for a behaviour-reading account of our results.

We argue, therefore, that monkeys instead succeeded in our study (and probably in other mind-reading studies) by using representations about what others perceive (i.e. in this case, that they are either hearing or not hearing an alerting sound). The present results add to a growing body of work indicating that apes (Hare et al. 2000, 2001; Tomasello et al. 2003; Call et al. 2004; Melis et al., in press), rhesus monkeys (Flombaum & Santos 2005) and capuchins, *Cebus apella* (D. E. Lyons & L. R. Santos, unpublished data) can reason about the minds of others when tested using experimental methodologies that require competition (see also Hare & Tomasello 2004; Santos et al., in press). Primates' successes in competitive tasks seem to come in contrast to poor performance on a number of mind-reading tasks that do not require competition (reviewed in Tomasello & Call 1997; Povinelli 2000).

Although primate researchers have yet to determine the root of this apparent dissociation between performance on competitive and noncompetitive tests, the general pattern fits well with the anecdotal literature on primate deceptive behaviour. Many anecdotes of primate deception entail situations involving competition between individuals over important resources, in which one individual has access to food, mates or some other commodity that it would prefer not to share with others. Rhesus monkeys at Cayo Santiago, for example, deceptively withhold food calls in the presence of high-quality foods that they would prefer not to share with competitors (Hauser 1992). A challenge for behavioural primatologists is to develop more experimental methods that mimic the competitive situations under which primates naturally display deceptive behaviours and to alter the features of these situations in experimentally meaningful ways (e.g. varying whether contested food or mates can be seen, what competitors do and do not know, etc.). In this way, researchers may be able to identify whether primates naturally commit deceptive acts with the intent to change the perceptions of others. Results from the present experiments suggest that such a discovery is more likely than some researchers might have believed.

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