ORIGINAL ARTICLE

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Do tufted capuchin monkeys (*Cebus apella*) spontaneously deceive opponents? A preliminary analysis of an experimental food-competition contest between monkeys

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Abstract A new laboratory procedure which allows the study of deceptive behavior in nonhuman primates is described. Pairs of tufted capuchin monkeys faced each other in a food-competition contest. Two feeder boxes were placed between the monkeys. A piece of food was placed in one of the boxes. The subordinate individual was able to see the food and to open the box to obtain the bait. A dominant male was unable to see the food or to open the box but was able to take the food once the box was opened by the subordinate. In experiment 1, two of four subordinate monkeys spontaneously started to open the unbaited box first with increasing frequency. Experiment 2 confirmed that this "deceptive" act was not due to a drop in the rate of reinforcement caused by the usurping dominant male, under the situation in which food sometimes automatically dropped from the opened box. In experiment 3, two subordinate monkeys were rerun in the same situation as experiment 1. One of them showed some recovery of the "deceptive" act but the other did not; instead the latter tended to position himself on the side where there was no food before he started to open the box. Although the results do not clearly indicate spontaneous deception, we suggest that operationally defined spontaneous deceptive behaviors in monkeys can be analyzed with experimental procedures such as those used here.

Keywords Social intelligence \cdot Tufted capuchin monkeys \cdot Deception

Introduction

In their seminal book, *Machiavellian Intelligence*, Byrne and Whiten (1988) proposed that advanced human intelli-

K. Fujita () · H. Kuroshima · T. Masuda Department of Psychology, Graduate School of Letters, Kyoto University, Yoshida-honmachi, Sakyo, Kyoto 606-8501, Japan e-mail: fujita@psy.bun.kyoto-u.ac.jp, Tel.: +81-75-7532852, Fax: +81-75-7532852 gence has evolved through managing complicated and reactive social environments. If we accept this hypothesis, how nonhuman primates manipulate others through deception is one of the core issues in understanding the evolutionary background of human intelligence.

Deception may not require higher intelligence; for example, mimicry observed in many insects lacks flexibility and deceptive intention (strategic deception: Byrne 1995). However, the type of deception relevant to the evolution of intelligence involves withholding or actively conveying incorrect information to others, and this is what we intend to analyze in this paper.

Many anecdotal observations suggest that some nonhuman primates may show this type of deceptive behavior. For instance, Goodall (1986) reported that a weaning infant chimpanzee pretended to be scared of something to be allowed onto the mother's back. Goodall herself observed nothing scary in the vicinity. De Waal (1982) described how an adult male chimpanzee, who had been wounded in a fight against the alpha male, walked as if lame only in front of the alpha male. Byrne (1995) reported that a juvenile chacma baboon screamed as if he had been hurt by a female who was about to dig up a tuber, which resulted in his mother driving the female away and the juvenile eating the food. In a semi-naturalistic experiment, Menzel (1974) found that a chimpanzee who witnessed an experimenter hiding food deceptively led a dominant individual away from the food. Similar behavior was observed in another study in which chimpanzees did not know who had witnessed the food being hidden (Matsuzawa 1991). Even a non-ape species, the white-collared mangabey, has been reported to engage in similar behavior (Coussi-Korbel 1994). All of these episodes are suggestive but open to conflicting interpretations.

Several studies have analyzed operationally defined deceptive behaviors in more controlled settings. Woodruff and Premack (1979) trained four chimpanzees to point out a box containing food to a "cooperative" trainer. After many sessions in which a "competitive" trainer ate the food when he/she found it in the box, two of the subjects started to point to the empty box when the competitive trainer approached. Such differential pointing has also been demonstrated in tufted capuchin monkeys (Mitchell and Anderson 1997) and squirrel monkeys (Anderson et al., in press). Thus it is clear that nonhuman primates can learn to behave deceptively as a result of intensive training, but it is difficult to conclude that this "deceptive" behavior reflects intentionality as opposed to a simple conditional discrimination. Another problem is that the subjects in the above studies were trained to deceive humans. Nonhuman primates have been selected to behave adaptively in natural environments; thus they should be better at handling social situations involving conspecifics.

In this paper, we describe a new laboratory procedure which allows us to analyze an operationally defined deceptive behavior between nonhuman primate conspecifics. This behavior develops spontaneously across sessions without explicit training. Using such procedures we may be able to analyze the ability for deception by nonhuman primates in more detail through more systematic modification of relevant experimental parameters than is possible in naturalistic situations.

Experiment 1

We set up an experimental situation in which two individuals, one dominant and the other subordinate, faced each other to compete for a food item placed between them. A piece of food was deposited in one of two boxes located between the monkeys. Only the subordinate monkey was able to see the bait and to open the box to obtain the bait. However, the dominant monkey was able to usurp the bait once the box was opened. The subordinate monkey was able to distract the dominant monkey by opening the empty box first, before switching to the baited box. We analyzed how this tactic of "reverse opening", the operationally defined "deceptive" behavior in this situation, would develop as the contest was repeated without any explicit training.

Methods

Subjects

Five tufted capuchin monkeys (*Cebus apella*) provided by the Primate Research Institute, Kyoto University, by way of its Cooperative Research Program, participated. They were kept in a group cage measuring 180 cm (width)×75 cm (depth)×230 cm (height). The dominant individual, Heiji, was a 6-year-old male, who played the role of "robber". The four subordinate monkeys were Zilla (6-yearold female), Kiki (4-year-old female), Theta (4-year-old female), and Pigmon (2-year-old male); they performed the role of "opener". All the monkeys had experience of a matching-to-sample task using a touch panel, and all except Pigmon had experienced object-choice experiments involving human attention cues (Vick and Anderson 2000). Zilla was pregnant at the start of the study and gave birth after experiment 1. The subjects were not deprived of food. They were given a full ration in the evening after all the scheduled experiments were completed. For the experimental sessions, the subjects were transported to an experimental cage in the adjacent room using a small transport box.

Apparatus

Two acrylic experimental cages measuring 46 cm (width)× 46 cm (depth)×52 cm (height) were used. The front wall of each cage had an opening 10 cm (height)×4.5 cm (width) at either side to allow the subjects to reach for objects placed outside of the cage. The bottom of the opening was 22 cm from floor level and the side of the opening was 3 cm from the side panel of the cage. The two openings were 31 cm apart. The front walls of the cages faced each other. Two feeder boxes measuring 13 cm (width)×11 cm (depth)× 6 cm (height) were placed between the cages. Each feeder box was directly in front of each opening of the cage, 9–12 cm from the dominant monkey and 17–27 cm from the subordinate. These distances were adjusted with regard to the body size and behavior of the subjects. A schematic illustration of the experimental setup appears in Fig. 1.

The feeder box (Fig. 2) was devised to meet the following three conditions: (1) it was easily opened from one side but hard to open from the other side; (2) the food in the box was visible only from the opener's side; (3) once the box had been opened, the opener could grasp the food quickly but the opponent required more time to do this. The lid of the box slid downwards when a small handle attached to the lid was pulled upwards. The box was made of transparent acrylic board but all parts except the lid were covered by opaque sticky tape. The bait was placed in the box out of view of the dominant monkey.

A large opaque board and a large transparent board were used to physically and/or visually isolate the monkeys from the feeder box during intertrial intervals and the baiting process.

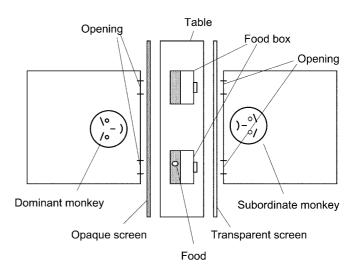


Fig.1 A schematic drawing of the experimental setup

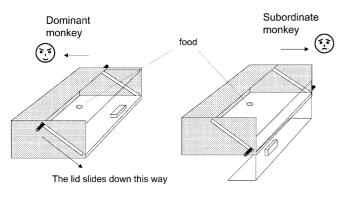


Fig.2 The food box used in experiment 1. *Food* is visible and the *lid* can be opened only from the side of the subordinate monkey

Procedure

Preliminary training. Heiji, the dominant monkey, was trained to pick up a piece of food, apple or sweet potato, from the opened feeder box by groping "blindly". Two fully transparent boxes were placed with the no-lid side towards the monkey in the experimental cage so that the monkey could not open the box himself. The experimenter showed a food item to the monkey and then opened the lid of one of the boxes, placed the food inside, then closed the lid. About 5 s later the experimenter opened the baited box again and allowed the monkey to grope inside it. Across sessions the no-lid side of the boxes was gradually rendered opaque by increasing the area covered by sticky tape. This training was conducted opportunistically for 2 weeks until the monkey consistently obtained the bait. Subsequently, the experimenter placed the opaque screen between the monkey and the feeder boxes before hiding the food. After removing the screen the experimenter opened the baited feeder. Twentytwo sessions of 20 trials were conducted until the monkey readily obtained the food from the opened baited box.

The four subordinate monkeys were individually trained to open the baited feeder box by pulling the handle on the lid to obtain the bait. After the monkeys were trained to open the box and retrieving the food, two boxes were placed with the lid side facing the subject in the experimental cage. The experimenter placed the transparent screen between the monkey and the boxes. Next the experimenter placed a piece of food in one box. About 5 s later, the screen was removed and the monkey was allowed to open the baited feeder. Daily sessions of 20 trials were conducted until the monkeys opened the baited feeder on every trial. This training required 20, 19, 18, and 18 sessions for Zilla, Kiki, Theta, and Pigmon, respectively.

Contest. Two monkeys, one dominant (Heiji) and the other subordinate, were placed in the experimental cages (see Fig. 1). Two feeder boxes were placed with the lid side facing the subordinate. The experimenter first placed the opaque screen between the dominant monkey and the boxes and the transparent screen between the subordinate monkey and the boxes. The experimenter next deposited a piece of food in one box. The trial started with removal of

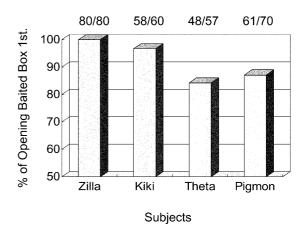


Fig. 3 Proportion of occasions on which the baited feeder was opened first during all sessions of experiment 1

the opaque screen; the dominant monkey was on standby. Five seconds later the transparent screen was removed, and the subordinate monkey was allowed to open the boxes. The trial ended when one of the monkeys obtained the bait. Sessions consisted of ten trials. The location (left or right) of the baited box was randomized across trials at 50% probability. Trials were filmed using three video cameras, one from behind the subordinate monkey to record the dominant's behavior, one from behind the dominant to record the subordinate's behavior, and the third from a lateral position to record the overall scene (Sony, CCD-SC65, CCD-TR3000, and CCD-TRV90). Zilla, Kiki, Theta, and Pigmon participated in eight, six, six, and seven daily sessions, respectively, while Heiji, the dominant male, participated in every session.

Results and discussion

All the subordinate monkeys learned to open the baited box first on 100% of trials in the last six sessions of preliminary training (i.e., 120 trials).

Figure 3 shows the percentage of openings of the baited box first by each subordinate monkey across all sessions. Zilla opened the baited box first in all 80 trials. Kiki did so in 58 out of 60 trials. However, the remaining two monkeys opened the unbaited box first in over 10% of the trials (Theta: 9 out of 57, Pigmon: 9 out of 70 trials). This behavior is hereafter referred to as "reverse opening". Theta performed reverse opening for the first time on the 13th trial (2nd session), while Pigmon did so on the 22nd trial (3rd session). The number of times reverse opening was observed in each session appears in Table 1.

There are at least two possible interpretations of fairly consistent reverse opening by two monkeys. One is that the monkeys were spontaneously trying to deceive the opponent. The other is that the monkeys' performances became more erratic due to the decreased probability of reward because of the usurping dominant opponent. Experiment 2 addressed the latter possibility.

Table 1 The number of training trials (*TR*) and reverse opening trials (*RO*) for Theta and Pigmon in each session of experiment 1

Subject	TR	Session							
		1	2	3	4	5	6	7	Total
Theta	TR RO	10 0	7 1	10 5	10 1	10 0	10 2		57 9
Pigmon	TR RO	10 0	10 0	10 2		10 3	10 1	10 2	70 9

Experiment 2

In order to test the effects of a decrease in the probability of reward on box-opening behavior, we devised a situation where there was no opponent but the probability of reward was controlled.

Methods

Subjects

Subjects were the two monkeys who consistently performed reverse opening in experiment 1, Theta and Pigmon.

Apparatus

We slightly modified the feeder boxes, as shown in Fig.4. A small hole was opened at the bottom. This hole was usually plugged by a magnetic plate. The food was placed directly on this plate. When a string from the handle of the lid was tied to a hook on the underside of the plate, opening the lid of the box resulted in instantaneous loss of the food. However, when the same string was tied to the hook attached to the bottom of the feeder box, opening the lid gave access to the food.

Other conditions were the same as in experiment 1 except that the dominant monkey was not used.

Procedure

The experimenter first placed both screens between the feeder boxes and the subject. The experimenter then baited one of the boxes and tied the string from the lid-handle to one of the two hooks under the box, depending on whether the particular trial was a baited trial or an unbaited trial. The string was always tied to the hook attached to the bottom of the box on the unbaited box. Next the trial was started by removing the opaque screen. The transparent screen was removed 5 s later. Trials ended when the subject obtained or lost the reward.

The probability of reward was 70% for Theta and 60% for Pigmon, which simulated their respective probabilities of obtaining the reward in the last five sessions of experiment 1 (70% and 64%, respectively). The "win" trials and

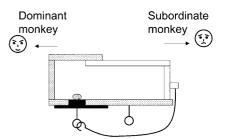


Fig.4 The modified feeder box used in experiments 2 and 3. *Food* may be lost when the *lid* is opened

"loss" trials appeared randomly during the session. Sessions consisted of ten trials. Theta received four sessions and Pigmon received six sessions.

Results and discussion

Figure 5 shows the percentage of openings of the baited box first by each subject in the last five sessions of experiment 1 (leftmost bar) and in all sessions of experiment 2 (middle bar). The rightmost bars concern experiment 3, which will be described later.

The frequency of reverse openings decreased drastically in this experiment. Pigmon never opened the unbaited box first and Theta did so only twice. The difference in the number of reverse openings between experiments 1 and 2 was statistically significant for both subjects (Pigmon: $\chi^2_{(1)}=11.76$, *P*=0.001; Theta: $\chi^2_{(1)}=3.92$, *P*=0.048). Thus the monkeys performed more "honestly" in this experiment than in experiment 1.

The decrease in the frequency of reverse opening suggests that the spontaneous emergence of reverse opening observed in the two monkeys in experiment 1 was not a simple consequence of decreased probability of reward caused by the behavior of the dominant opponent.

The feeder boxes used in experiment 2 had a slightly different appearance from those in experiment 1. This might have affected the monkeys' performances. This problem was addressed in the next experiment, which reintroduced the dominant monkey into the contest.

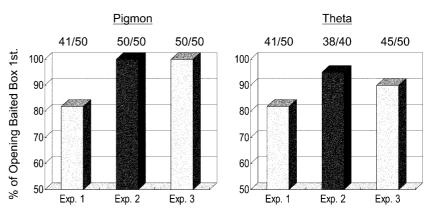
Experiment 3

Experiment 3 replicated experiment 1 with the use of the new feeder boxes introduced in experiment 2.

Methods

Subjects

The same monkeys who participated in experiment 2, Theta and Pigmon, participated as openers and the dominant male, Heiji, again participated as robber.



Apparatus

ment 3

The feeder boxes used in experiment 2 were used, but the magnetic plate at the bottom of the feeder was fixed so as not to affect the food. Other conditions were exactly the same as in experiment 1.

Procedure

The procedure was exactly the same as in experiment 1. Theta participated in 5 sessions and Pigmon participated in 12 sessions. These subjects received one session per day. Heiji, the dominant male participated in all sessions.

Results and discussion

The rightmost bars in Fig. 5 show the percentage of openings of the baited box first during the first five sessions.

Theta's reverse opening recovered; she opened the unbaited box first 5 times out of 50 trials, a frequency not significatly different from that in experiment 1 ($\chi^2_{(1)}=1.64$, P=0.200, ns). This result reinforces the possibility that reverse opening by Theta in experiment 1 may have been a deceptive behavior. However, two additional observations cast some doubts on this view. First, Theta's overall win rate was 70% in the last five sessions of experiment 1, but her win rate when she performed reverse opening was lower, five out of nine. Moreover, she lost in all five reverse-opened trials during experiment 3. In other words Theta gained nothing by her "deceptive" behavior. It could be argued that she tried to deceive, only to fail. However, an additional observation of her behavior during reverse opening raises further doubt. A deceiver should presumably be quick to open the baited box after attracting the opponent to the false location. But Theta's behavior after opening the unbaited box was not always like that. Analysis of videos of her behavior on "deceptive" trials revealed that her latency to open the baited box after opening the unbaited one averaged 2.96 s (range: 0.7-7.7) in experiment 1 and 4.0 s (range: 3.0–5.3) in experiment 3. She sometimes simply watched while the opponent groped in the opened box. Thus it is difficult to conclude whether Theta's reverse opening reflects deceptive intent or not.

In contrast, Pigmon always opened the baited box first in experiment 3. The frequency of reverse opening decreased significantly from the last 5 sessions of experiment 1 ($\chi^2_{(1)}$ =11.76, *P*=0.001). Pigmon performed reverse opening only once, in the seventh session. It is possible that he tried to deceive only in experiment 1. His win rate on reverse opening trials was seven out of nine, which is slightly higher than his overall winning rate (64%) during the last 5 sessions of experiment 1, but the difference was not statistically significant ($\chi^2_{(1)}$ =0.90, *P*=0.343, ns). Thus Pigmon also gained nothing through "deceptive" behavior. His average latency to opening the baited box after opening the unbaited one was 4.1 s (range: 2.0–9.9) in experiment 1. This slow behavior indicates failure to switch to the baited box quickly after the reverse opening.

Results of additional video analyses

The following two additional video analyses were conducted in order to examine the possibility of deception by means other than reverse opening.

Latencies to opening the feeder box after removal of the transparent screen

The monkeys might have opened the box when the opponent was not attending, perhaps withholding information about the location of the food. To assess these possibilities, we analyzed the video records for latencies to opening the box after the transparent screen was removed. If the subordinates tried to withhold information and/or to check if the opponent was attending or not, latencies should be longer in situations with the opponent than in those without the opponent.

Median latencies for Pigmon in the three experiments were 2.49 (last 5 sessions), 1.82 (all 6 sessions), and 1.95 (first 5 sessions) for experiments 1, 2, and 3, respectively. Although he showed the shortest latency in the situation without the opponent (experiment 2), this difference was not significant ($H_{(2)}$ =4.51, n=160, P=0.101, ns, Kruskal-Wallis test). On the other hand, Theta's latencies varied significantly; 1.22 (last 5 sessions), 1.89 (all 4 sessions),

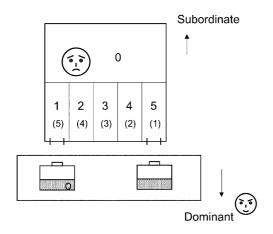


Fig. 6 Codes used to analyze position of the subordinate monkeys. Positions are *numbered* 1–5 from the side close to the baited box

and 1.27 (all 5 sessions), for experiments 1, 2, and 3, respectively ($H_{(2)}$ =7.22, n=137, P=0.027, Kruskal-Wallis test), with the slowest responses in experiment 2. Thus, the latency data provide no evidence that the monkeys changed their behavior in favor of deception as a function of the presence of the opponent.

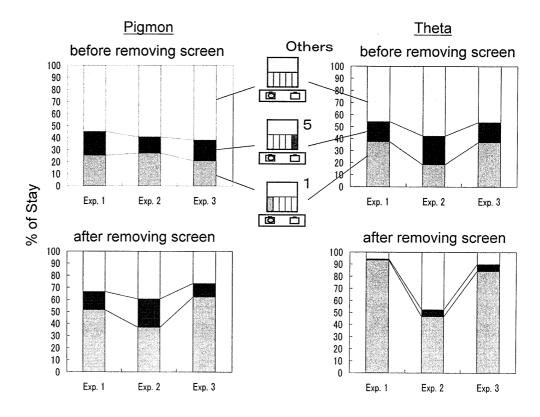
The subordinates' positions before and after the removal of the transparent screen

It was hypothesized that a subordinate monkey might try to either withhold information or provide false information during the 5 s between removal of the opaque screen in front of the opponent and removal of the transparent screen in front of the subordinate, during which the subordinate was able to see the opponent but not reach for the boxes.

For all three experiments the positions of the subordinate monkeys during 5 s before and after removal of the transparent screen were encoded as shown in Fig. 6. The half of the test cage farthest from the feeder boxes was numbered 0. The other half was divided into five zones numbered 1 through 5 in increasing distance from the baited box. The position of the head of the monkey was sampled every 0.5 s.

Figure 7 shows relative percentage of time in positions 1 (closest to the bait) through 5 (farthest). For Pigmon the relative percentage in zone 5, farthest from the baited box, before removal of the transparent screen (top graph) was higher in situations with the opponent (experiments 1 and 3) than with no opponent (experiment 2). This variation was statistically significant ($\chi^2_{(2)}=10.0$, *P*=0.007, between experiments 1 and 2; $\chi^2_{(2)}$ =9.98, P=0.007, between experiments 2 and 3), suggesting that this monkey tended to take up position away from the baited box before responding only in the presence of the dominant male. This tendency was reversed after removal of the screen (botttom graph) ($\chi^2_{(2)}$ =27.1, P<0.001, between experiments 1 and 2; $\chi^2_{(2)}$ =50.4, P<0.001, between experiments 2 and 3). Thus, Pigmon may have tried to give the opponent false information before opening the baited box. On the other hand, no such differential positioning before and after removal of the transparent screen was observed in Theta; she always positioned herself "honestly" near the bait more often in the presence of the dominant opponent than

Fig.7 Positioning of the subordinate monkeys before (*above*) and after (*below*) the transparent screen was removed to allow response



in his absence (before removal of the screen: $\chi^2_{(2)}=39.0$, P<0.001, between experiments 1 and 2, and $\chi^2_{(2)}=33.0$, P<0.001, between experiments 2 and 3; after removal of the screen: $\chi^2_{(2)}=66.8$, P<0.001, and $\chi^2_{(2)}=58.0$, P<0.001, respectively).

General discussion

In experiment 1, in a situation where two monkeys, dominant and subordinate, competed for food, two of four subordinate monkeys spontaneously started to open the unbaited box first (reverse opening) with some consistency. Experiment 2, in which the same two subjects were tested without the opponent and in which the probability of reward was controlled by the experimenter, confirmed that reverse opening was not simply due to a decrease in the rate of obtaining the bait caused by the presence of the dominant opponent. Experiment 3 was a partial replication of experiment 1; one monkey again showed reverse opening but the other monkey did not.

Viewing the overall results, at least one monkey may have tried to deceive her opponent. But as noted above, there was almost no detectable benefit derived from reverse opening in terms of win rate, and behavior following reverse opening was not consistent with a deceptive strategy. In short, the behavior does not seem to have been effective as a deceptive tactic.

One of the monkeys, Pigmon, may have adopted a weaker tactic of taking up the position farthest from the bait before opening the baited box. He might thus have avoided serious competition with the dominant male, and later punishment in the home cage. Casual observations suggested that there was more aggression in the home cage after the start of this study than before, and one female, Zilla, was injured on the arm; previously such events were rare in this group. But it is also possible that Pigmon was simply avoiding the dominant and potentially threatening opponent in the experimental cage.

One problem with this series of experiments may be that the time the subordinates stood to gain by reverse opening was too short to increase the potential benefit resulting from this tactic, as the distance between the food boxes was short and it was easy for the dominant male to switch from one box to the other. The subordinate monkeys might conceivably engage in more deception if the benefit is larger than the potential risks they may face in the home cage.

In this study the operationally defined deceptive behavior was to provide false information to the opponent. In human children, simply concealing information seems to develop earlier than providing misleading information (LaFrenière 1988). Byrne (1995) noted four episodes of deceptive behavior by Cebidae monkeys but three of them consisted of concealment. In chimpanzees, on the other hand, most episodes involved distracting/attracting attention of the others. We may be more likely to observe the emergence of deception if we devise an experimental situation in which the monkeys stand to benefit from concealing information. The deceptive behavior aimed for in this study may have been too cognitively demanding.

In summary, the results obtained in this study failed to demonstrate a clear example of spontaneous deception in capuchin monkeys. The behaviors shown by the monkeys were not conclusive and the benefit of the deceptive behavior to the deceiver was not clear. Nevertheless, the data were not completely negative, either, and there remains a possibility that capuchin monkeys might be capable of spontaneously providing false information in situations where they compete for food. At the least, this study demonstrates that in competitive situations such as the one used here we can analyze operationally defined spontaneous deceptive behavior of nonhuman primates in the laboratory.

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