

Ring-tailed lemurs (*Lemur catta*) exploit information about what others can see but not what they can hear

Joel Bray · Christopher Krupenye ·
Brian Hare

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Abstract Studies suggest that haplorhine primates are sensitive to what others can see and hear. Using two experimental designs, we tested the hypothesis that ring-tailed lemurs ($N = 16$) are also sensitive to the visual and auditory perception of others. In the first task, we used a go/no-go design that required lemurs to exploit only auditory information. In the second task, we used a forced-choice design where lemurs competed against a human who would prevent them from obtaining food if their approaches were detected. Subjects were given the choice of obtaining food silently or noisily when the competitor's back was turned. They were also given the choice to obtain food when the competitor could either see them or not. Here, we replicate the findings of previous studies indicating that ring-tailed lemurs are sensitive to whether they can be seen; however, we found no evidence that subjects are sensitive to whether others can hear them. Our findings suggest that ring-tailed lemurs converge with haplorhine primates only in their sensitivity to the visual information of others. The results emphasize the importance of investigating social cognition across sensory domains in order to elucidate the cognitive mechanisms that underlie apparently complex social behavior. These findings also suggest that the social dynamics of haplorhine groups impose

greater cognitive demands than lemur groups, despite similarities in total group size.

Keywords Social cognition · Social intelligence hypothesis · Sensory domains · Perspective taking

Introduction

The social intelligence hypothesis proposes that the challenges of living in a group have selected for cognitive skills to compete with conspecifics for mates and resources (Jolly 1966; Humphrey 1976; Kummer et al. 1997; Dunbar 2003; Byrne and Bates 2007). This hypothesis implicates the large and complex nature of primate social groups as a major driving force in primate cognitive evolution. One proposed mechanism that could help animals navigate this social arena is knowledge of others' psychological states. For example, understanding that others have perceptions, beliefs, and intentions would allow an animal to better predict and manipulate the behavior of conspecifics (Byrne and Whiten 1988; Cheney and Seyfarth 1990; Kummer et al. 1997).

Numerous studies with nonhuman apes and monkeys, especially chimpanzees (*Pan troglodytes*) and rhesus macaques (*Macaca mulatta*), have demonstrated that some species comprehend particular psychological states of others (Hare et al. 2000, 2001, 2006; Call et al. 2004; Flombaum and Santos 2005; Melis et al. 2006; Santos et al. 2006; Bräuer et al. 2007; Kaminski et al. 2008; Phillips et al. 2009; Martcorena et al. 2011; Crockford et al. 2012; MacLean and Hare 2012). However, haplorhines—monkeys and apes—may share social-cognitive skills due to homology rather than from independent evolutionary events, making it difficult to definitively test the social intelligence hypothesis within the haplorhine clade

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J. Bray (✉) · C. Krupenye · B. Hare
Department of Evolutionary Anthropology, Duke University,
104 Biological Sciences, Box 90383, Durham, NC 27708, USA
e-mail: joel.bray@duke.edu

B. Hare
Center for Cognitive Neuroscience, Duke University, Durham,
NC, USA

(MacLean et al. 2011, 2013). Haplorhines also vary widely on many aspects of life history, including brain size, potentially confounding any result (Kappeler and Pereira 2003). In contrast, strepsirrhines, particularly lemurs, exhibit great interspecific diversity in group size and social behavior while retaining close genetic similarities (Perelman et al. 2011). For example, despite having very similar life history characteristics, a wide range of social systems exists within the Lemuriforme clade, including pair-bonded species, species with groups of several adult males and females, and even species that have a fission–fusion system (Mittermeier and Nash 2010). Thus, it is likely that any species differences between lemurs are a result of recent adaptations to different socioecological niches.

Lemurs diverged from the rest of the strepsirrhine lineage approximately 68.7 million years ago (Perelman et al. 2011). Although most lemur species live in small social groups, ring-tailed lemurs (*Lemur catta*) live in large multi-male/multi-female groups that resemble the social environment of Old World monkeys (Jolly 1966; Sauther et al. 1999). Recently, Sandel et al. (2011) and MacLean et al. (2013) tested the social intelligence hypothesis with lemurs using cognitive tasks that required subjects to exploit positional cues, such as the head orientation of a human competitor, in order to pilfer food. In both studies, ring-tailed lemurs outperformed closely related species that live in smaller social groups, suggesting that the large group size of ring-tailed lemurs may have led to convergence with haplorhine primates.

Notably, most of the studies evaluating social-cognitive abilities have been conducted in the visual sensory domain. In recent years, researchers have begun to ask whether these cognitive abilities are limited to the visual domain, or whether they generalize to the auditory domain as well (primates: Melis et al. 2006; Santos et al. 2006; Bräuer et al. 2008, 2012; dogs: Kundery et al. 2010). As exclusively auditory cues are by their nature indistinguishable visually, success in auditory tasks likely requires greater cognitive sophistication, since subjects must represent the auditory features of the apparatus separate from the social aspects of the task. In contrast, the visual information in the tasks discussed above is intrinsically social for species that rely heavily on sight. Indeed, lemurs in these studies may have been following relatively simple egocentric rules (e.g., avoid faces), rather than relying on any cognitive representation of the competitor's visual perspective.

Within primates, both chimpanzees and rhesus macaques have displayed an understanding of what another individual can hear, suggesting that the social-cognitive abilities of haplorhine primates are flexible across domains (Melis et al. 2006; Santos et al. 2006). In each study, subjects were presented with two food options.

Acquiring the “noisy” option would create a noise in the process, alerting a human competitor to the subject's presence, while the alternative “silent” option could be obtained silently. Specifically, rhesus macaques in Santos et al. (2006) were given a choice to steal food from one of two containers with hinged lids. A human experimenter stood behind the containers, with his head and body oriented away from the containers so that he could not see them. If the subject retrieved food from the “noisy” option, bells attached to the lid would ring and alert the experimenter to her presence. The “silent” option was identical except that the ringers in the bells were removed, so stealing food from this container would not reveal the subject's presence. In this condition, rhesus macaques showed a significant preference for the silent option. To ensure that the macaques were not simply averse to the noise, independent of the experimenter's perceptual state, a control condition featured the human experimenter facing the two food options. In this condition, the auditory cues were irrelevant to whether the experimenter was aware of the macaques' presence, and the macaques did not show a significant preference for either option.

In this study, we chose to test ring-tailed lemurs since they are thought to have the most haplorhine-like social system and have shown the most success in previous social-cognitive experiments (Sandel et al. 2011; MacLean et al. 2013). However, there are competing explanations for lemurs' successful performance in previous studies. One possibility is that they can in fact flexibly respond to the perception of others in a range of novel contexts. The alternative low-level hypothesis is that they simply apply an inflexible behavioral rule to avoid faces. To test these hypotheses, we designed two experiments, based on the methods of Santos et al. (2006) that required subjects to exploit auditory information. If ring-tailed lemurs have converged with haplorhines in the mechanism used to solve social competition problems, then they, like haplorhines, should exploit information about what others can hear in the present task. Alternatively, if ring-tailed lemurs converge with haplorhines only in behavior but use a different mechanism in visual tasks, then they should not be able to solve the present task due to an inability to mentally represent what others can hear.

Experiment 1

In Experiment 1, we tested ring-tailed lemurs' tendency to approach a single box, baited with food and proximate to a human competitor. Each subject received two sessions over separate days. In one session, the box was rigged to make noise when the lemur attempted to retrieve the food

(“noisy” condition); in the other session, the box did not make noise (“silent” condition). The human, facing away from the box, would turn around and remove the food if the subjects approached in either condition. We predicted that if lemurs were making an implicit connection between the noise-producing capabilities of the box and the competitor’s auditory perception, they would approach less in the noisy condition (and/or show greater latency in their approaches) by imputing the competitor’s behavioral response to the noise of the box. In contrast, no clear causal relationship existed in the silent condition.

Methods

Subjects

We tested 10 ring-tailed lemurs, one of whom had been tested in a previous social-cognitive study (Table S1 in Online Resource 1). Lemurs were housed either in pairs or groups in indoor enclosures at the Duke Lemur Center in Durham, NC, USA, although some had occasional access to semi-free-ranging outdoor enclosures as well. All subjects were tested in their indoor home enclosure, physically separated from all group members for the duration of the session. Food was temporarily removed (aside from primate biscuits, which are nonpreferred items); however, subjects were not food-restricted before testing, and water was available ad libitum.

Apparatus

Lemurs were tested on an elevated platform ($79 \times 122 \times 122$ cm, $H \times L \times W$). One of three (motivational, silent, or noisy) rectangular boxes ($16 \times 23 \times 16$ cm, $H \times L \times W$), made of transparent plastic, was centered on one side of the platform, and a plastic plate (13.5×13.5 cm) was centered on the opposite side (Fig. 1). All boxes were open in the front and back. A thin rectangular barrier (1.5×5 cm, $H \times L$) was placed 4 cm from the back of the box. Food was placed behind this barrier during test trials. The barrier prevented subjects from making a quick reach for the food, giving the experimenter sufficient time to take food away on trials when doing so was necessary. All three boxes were identical save for a modification to the front of the silent and noisy boxes (Figure S1 in Online Resource 1). On these boxes, an additional “door flap” (12×12 cm, $H \times W$) was attached to the top of the front entrance and extended 2 cm from the bottom of the box. The flap was made of a thin, transparent plastic sleeve. Three bells were attached in vertical columns on each side of the flap (total of six bells) so that they did not touch and could not move. On the silent box, the ringers in the bells were removed, so that brushing against the flap produced no noise. The bells were left intact

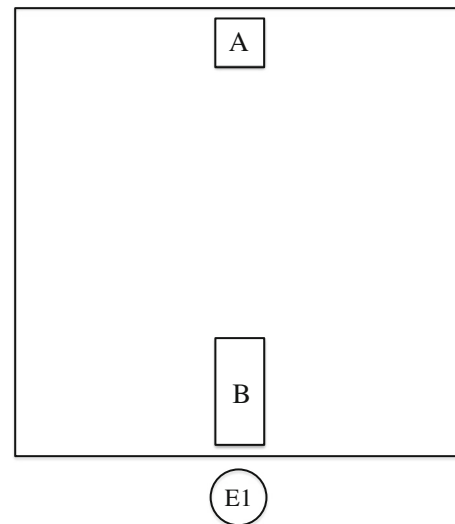


Fig. 1 Schematic of the platform used in Experiment 1 (from *above*). Subjects were centered at a *plate* (A) at the beginning of each trial. Subjects were then allowed to attempt to retrieve food from a *box* (B). Experimenter 1 (E1) sat behind *box* B

on the noisy box, so that brushing against the flap caused the bells to ring. The motivational box had no bells or sleeve.

Procedure

The experiment consisted of two conditions: noisy and silent. All subjects completed both conditions, and each condition was conducted on a separate day (range: 2–10 days apart). In each condition, either the noisy or silent box was used, depending on the respective condition. The order in which subjects received each condition was counterbalanced. Each condition consisted of three phases: (1) an introductory phase, (2) pretest, and (3) test.

The introductory phase itself had two parts. The first part (“familiarization”) consisted of 8 trials, an example of which can be viewed in Online Resource 2. A transparent square of plastic was attached to the back of the box (silent or noisy depending on the condition) during this phase to require subjects to retrieve food from the front of the box. First, subjects were attracted to the centering plate opposite the box at the beginning of each trial, on which the experimenter (E1) placed a single piece of grape using an elongated spoon. The trial began once the subject consumed the piece of grape. For each of the first 5 trials, the box was baited with 3 pieces of grape: behind the barrier, in front of the barrier, and just inside the front entrance (Figure S2 in Online Resource 1). In the final 3 trials, the box was baited with a single piece of grape, behind the barrier. In each trial, E1 left the room after baiting and subjects were given 1 min to retrieve as much food as was available. Any or all of the 8 trials could be repeated a maximum of one time if the subject failed to retrieve all of the available food within 1 min. To advance to

the second part of the introductory phase, subjects were required to retrieve the single piece available on the final 3 trials. This phase ensured that the subject was comfortable with retrieving food from the box.

The second part of the introductory phase consisted of a single “baseline” trial, adopted from Sandel et al. (2011), to ensure that the lemur would retrieve food with E1 in the room before beginning the other phases. Once the subject was centered (again with a piece of grape at the centering plate), E1 placed a second piece of grape on a plate opposite the centering plate (adjacent to E1) and then turned away from the subject, while still standing, until the lemur retrieved the food. To advance to the pretest, the subject had to retrieve the food within 2 min, but the trial could be repeated a maximum of one time if no approach was made. If the subject did not pass either part of the introductory phase, the session was aborted. The subject was eligible to be tested another day, beginning again with the introductory phase of the same condition.

The pretest, also adopted from Sandel et al. (2011), consisted of 4 trials and served to establish E1 as a competitor. An example trial can be viewed in Online Resource 2. E1 placed two baited food plates on opposite sides of the table from each other and equidistant from the centering plate. E1 then sat on a stool directly behind one of the plates with his face level to the plate. The subject was given 2 min to make a first approach. If the subject first approached the food in front of E1 (“contested” food), he removed the plate from the table. The subject was then allowed 1 min to retrieve food from the uncontested plate. If the subject first approached the uncontested food, she was allowed to feed and was then given 1 min to approach the contested food. If the subject approached the contested food as a second choice, E1 removed the plate. Subjects were scored as having approached a food plate if their head or hand came within 12 cm of the plate, indicated by a pencil line drawn on the platform. The location of E1 was counterbalanced within subjects. To advance to the test trials, lemurs were required to first approach the uncontested food on the final 3 pretest trials. If a subject failed to meet this criterion, a second pretest was administered. However, no more than two pretest sessions were conducted on any day to ensure motivation throughout the entire experiment. Any trial during the pretest was repeated once if the subject did not approach either side after 2 min. After two trials of nonapproach on any given trial, the session was aborted. (One subject, due to scheduling issues, was allowed a third attempt on trial 4 and successfully approached.)

In the test, 12 motivational and 12 competitive trials were administered, for a total of 24 trials per condition (see Online Resource 3 for examples). Motivational trials were identical between conditions, and only the type of box (noisy or silent) differed between conditions on the competitive trials. Motivational and competitive trials were

given in blocks of two, and the order of the blocks was counterbalanced between subjects. On the motivational trials, E1 baited the centering plate followed by the box. Sitting directly behind the box, E1 then turned his body to face away from the subject. The subject was allowed 2 min to approach and retrieve the food. These trials were designed to keep the subjects engaged and motivated to continue with the experiment. They also ensured that a nonapproach on competitive trials was not out of general disinterest or confusion about where to find food.

On the competitive trials, in both the noisy and silent conditions, E1 again sat with his body facing away from the box but took food away as soon as the subject pushed against the door flap, causing the bells to ring in the noisy but not the silent condition. A video camera outside the room informed E1 to the lemur’s location in both conditions. As with the motivational trials, subjects were allowed 2 min to approach.

Scoring and analysis

Subjects were defined as having approached if they crossed the front threshold of the box. If subjects crossed the threshold of the box but did not retrieve food during a motivational trial, they were scored as approaching but given the remainder of the 2 min to retrieve the food (3 trials). Latency to approach was defined as starting when the subject had consumed the centering food and E1 had turned his back, and ending when the subject crossed the front threshold of the box. If the lemur did not attempt to retrieve the food within 2 min, the trial was marked as “no approach” and scored as 120 s for this analysis (i.e., the maximum time allotted for individuals to make a choice).

All trials were scored twice: live and from a video recording. In live coding, E1 scored whether subjects approached, and a second experimenter (E2) outside the testing room recorded latency using a stopwatch (always rounding down to the nearest whole second). Latency was not recorded live on seven trials due to experimenter error and scored after the session from video. In addition to the live scoring, someone blind to the experimental hypotheses coded every trial from video. The latency values from the coder were used for statistical analyses. Inter-observer reliability of whether or not subjects approached on each trial was 100 %. Latency measurements were also highly correlated (Pearson’s correlation = 1.0, $P < 0.01$). We used two-tailed Wilcoxon signed ranks tests to compare subjects’ frequencies of approach and latency measurements.

Results

Subjects approached on motivational trials significantly more than on competitive trials within both conditions (Wilcoxon test, *noisy*: $Z = -2.680$, $P = 0.007$, $r = 0.60$;

Table 1 Complete individual results for Experiment 1, including means and standard errors

Subject	Motivation approach—noisy (#)	Competitive approach—noisy (#)	Motivation approach—silent (#)	Competitive approach—silent (#)	Motivation latency—noisy (s)	Competitive latency—noisy (s)	Motivation latency—silent (s)	Competitive latency—silent (s)
Sierra Mist	8	4	6	4	42.1	81.3	61.3	81.1
Berisades	12	11	12	10	3.8	13.8	4.3	23.5
Aracus	12	12	12	12	3.1	3.2	3.8	3.5
Edelweiss	12	11	12	12	11.5	35.0	11.1	8.8
Liesl	8	3	5	4	44.8	94.3	81.5	81.2
Fritz	2	0	2	1	100.6	120	110.7	110.3
Tellus	10	6	11	8	28	82.8	33.6	68.3
Alexander	12	10	11	8	4.2	32.9	26.5	61.5
Fern	12	11	10	9	5.3	15.2	25.8	33.6
Lilah	10	3	11	7	28.5	96.9	16.8	71.3
Mean	9.8	7.1	9.2	7.5	27.2	57.5	37.5	54.3
SE	1.0	1.4	1.1	1.1	9.6	13.2	11.3	11.1

All values are reported as either the number of trials approached (out of 12) or in seconds

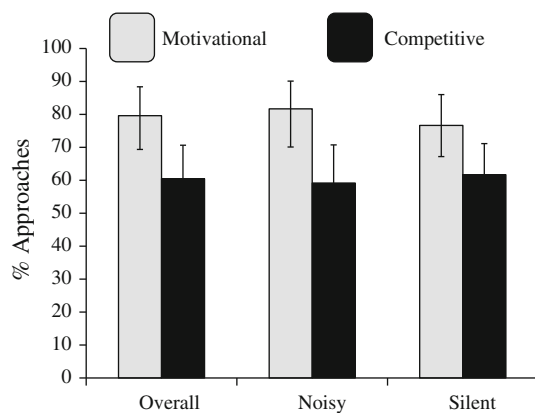


Fig. 2 Mean \pm SE percentage of trials that subjects approached on motivational and competitive trials in Experiment 1. Subjects approached significantly more on motivational trials than competitive trials in both conditions and overall. However, there was no significant difference in the frequency of approach on competitive trials between conditions

silent: $Z = -2.539$, $P = 0.011$, $r = 0.57$; Fig. 2; see Table 1 for individual results, means, and standard errors). Similarly, subjects approached faster on motivational than competitive trials in the noisy condition (Wilcoxon test, $Z = -2.803$, $P = 0.005$, $r = 0.63$), though the difference was not significant in the silent condition (Wilcoxon test, $Z = -1.785$, $P = 0.074$, $r = 0.40$). On competitive trials, however, subjects showed no difference in approach frequency between conditions (Wilcoxon test, $Z = -0.499$, $P = 0.62$, $r = 0.11$; Fig. 2), nor did their latencies differ (Wilcoxon test, $Z = -0.510$, $P = 0.61$, $r = 0.11$). There was also no significant difference in the number of approaches on competitive trials between the first and

second sessions (Wilcoxon test, $Z = -0.997$, $P = 0.32$, $r = 0.22$).

Discussion

Subjects approached less on competitive than on motivational trials, indicating that they made a distinction between the two types of boxes. This suggests that not approaching on any given competitive trial was not out of disinterest or uncertainty about where the food could be found. Anecdotally, lemurs often approached the box on competitive trials and looked inside before turning around and leaving the vicinity of the box, reinforcing that they were aware that food was present. Still, subjects made no distinction between the two conditions, approaching the noisy and silent boxes at comparable rates and with similar latencies. This suggests that lemurs are not sensitive to the auditory perception of others. However, the experimental design tested for an implicit behavioral response to the competitor's perception, which may not have been intuitive since it required subjects to inhibit approaching a single food option. In a second experiment, subjects were given a direct and explicit choice on each trial between a noisy and silent option.

Experiment 2

In Experiment 1, subjects did not exploit information relevant to the auditory perception of others, although only a single cue (noisy or silent) was present in each session. Species that showed success in previous experiments

(Melis et al. 2006; Santos et al. 2006) made choices between noisy and silent options simultaneously, which might make the distinction more salient. To address this possibility in Experiment 2, we conducted a task directly based off Santos et al. (2006) that presented subjects with a choice between a noisy and silent food option. We predicted that if lemurs are sensitive to the auditory perception of others, they should prefer the silent option.

Methods

Subjects

We tested 12 ring-tailed lemurs, six that had previously completed Experiment 1 and six that were naïve to both Experiment 1 and previous social-cognitive experiments (Table S1 in Online Resource 1). Housing and testing conditions were identical to Experiment 1.

Apparatus

Lemurs were tested on the same platform as in Experiment 1. Both the noisy and silent boxes were used simultaneously, one on each side of the platform. In contrast to Experiment 1, both boxes had opaque, hinged doors on the back to prevent subjects from accessing food from that direction. In addition, black tape covered the back 5 cm around the sides of each box, shielding the lemurs' view of the food from that angle and encouraging them to approach from the front. The boxes were also fastened to the table to ensure that subjects experienced them in a uniform manner.

Procedure

The experiment consisted of one session given on a single day. The session had three phases: (1) an introductory phase, (2) pretest, and (3) test. The familiarization part of the introductory phase was almost identical to Experiment 1, except that subjects were allowed to explore both the noisy and the silent box simultaneously instead of just one. However, only one box was baited on each trial. The first 4 trials used 3 pieces of food (same locations as Experiment 1), and the last 4 trials used 1 piece of food (located behind the barrier). Subjects were required to retrieve food on the final 4 trials. The location of the noisy and silent boxes was counterbalanced for each subject. The baseline trial and pretest were identical to Experiment 1.

The test phase was administered in four blocks of four trials (total = 16 trials). Blocks consisted of two non-competitive trials and two competitive trials, the latter including one trial where the experimenter (E1) could not see the platform (“face-back”) and one trial where E1 could see it (“face-forward”). Before each trial, E1 first

gently touched the flap of the box on the left and then on the right, demonstrating which box was noisy and which silent. Next, E1 baited the left box followed by the right. In the noncompetitive trials, E1 then baited the centering plate before crouching underneath the platform, out of view of the subject. Lemurs were allowed to feed from both boxes. The noncompetitive trials served two purposes. First, since they always preceded competitive trials within a given block, they gave subjects personal experience with both the noise-producing capabilities and the locations of each box. Second, the trials served to identify preference biases for location or box type in the absence of a competitor's proximity to the food.

In the face-back trial, E1 baited both boxes and then sat with his face centered and equidistant between the two boxes but directed away from the platform, so that neither of the boxes was visible to him (Fig. 3a). If the subject entered the noisy box, revealing her choice, E1 turned around and removed the food, and then took away the silent option as well. If the subject entered the silent box, then she was allowed to retrieve and eat the food. E1 then turned around and removed the noisy food option. In the face-forward trial, E1 faced the platform and could see both boxes, although he did not move his head to track the lemur's movements (Fig. 3b). If the subject entered either

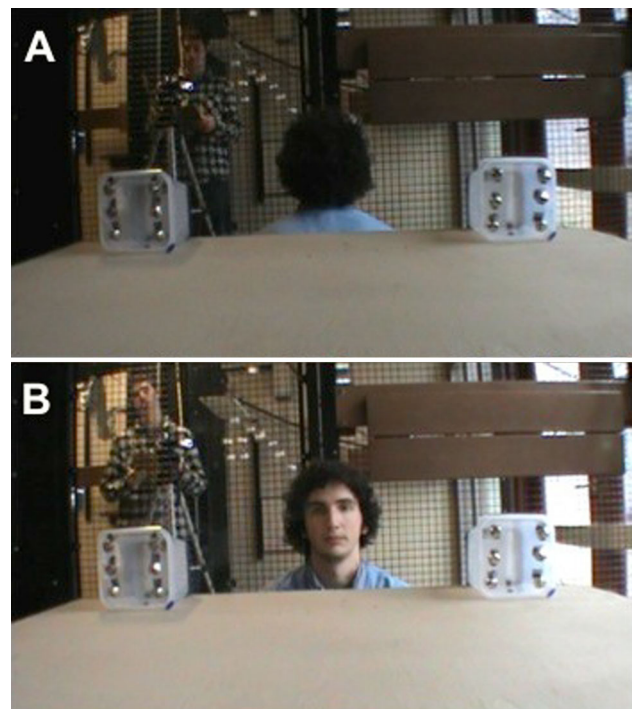


Fig. 3 In Experiment 2, subjects were given the choice to steal food from either a noisy or silent *box* on each competitive trial. In the face-back condition (**a**), the human competitor faced away from the subject and could not see either *box*. In the face-forward condition (**b**), the human competitor faced the subject and could see both *boxes*

box, E1 removed that piece of food first and then the other piece. Examples of face-back and face-forward trials are shown in Online Resource 4.

On all trials of the test, subjects were allowed 2 min to make an approach or acquire all available food. On non-competitive trials, if the subject crossed the threshold but the second experimenter (E2) could not determine whether food was retrieved, the subject was given the remainder of the 2 min to eat, as a precaution, and the box was checked after time was up. The locations of the noisy and silent boxes, and the order of the face-forward and face-back trials within each block, were counterbalanced between blocks for each subject. Within every block, however, both noncompetitive trials were always administered first. (Due to experimenter error, one subject received just 1 of 2 noncompetitive trials on her second block; she did approach on the other noncompetitive trial.)

Scoring and analysis

Subjects were defined as having approached if they crossed the front threshold of the box. If subjects crossed the threshold of a box but did not retrieve the food on non-competitive trials, that box was coded as their first choice, but they were given the remainder of the 2 min to retrieve all remaining food (3 trials). Latency to first choice was defined as starting when the subject had consumed the centering food and E1 was positioned, and ending when the subject crossed the front threshold of either box. If the lemur did not attempt to retrieve the food within 2 min, the trial was scored as “no approach,” again considered to be 120 s for this analysis. Parts of four noncompetitive trials were not scored live due to experimenter error and were coded after the session from video. All trials were scored a second time by a coder in an identical manner as Experiment 1. Latency values from the coder were used for statistical analyses. Inter-observer reliability of subjects’ first choice on each trial was 100 %. Latency values were also highly correlated (Pearson’s correlation = 0.998, $P < 0.01$).

We used two-tailed Wilcoxon signed ranks tests to compare frequencies of approach and latency measurements between conditions. We also compared subjects’ responses to chance (50 %) on the face-back, face-forward, and noncompetitive conditions using one-sample Wilcoxon signed rank tests; a first trial analysis was also done for the face-back condition.

Results

The two populations of ring-tailed lemurs (naïve and experienced) did not differ significantly on any response measure (Online Resource 1), so the two groups were

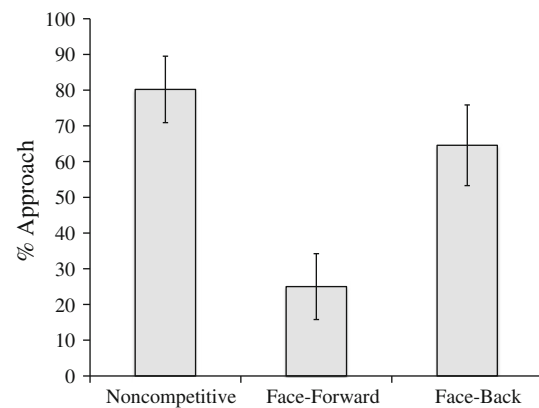


Fig. 4 Mean \pm SE percentage of trials that subjects approached either *box* for each condition of Experiment 2. Subjects approached significantly more on face-back than face-forward trials

lumped together for further analysis. Subjects approached significantly less in the face-forward than in both the non-competitive and face-back conditions (Wilcoxon test, *forward-noncompetitive*, $Z = -2.950$, $P = 0.003$, $r = 0.60$; *forward-back*, $Z = -2.379$, $P = 0.017$, $r = 0.48$; Fig. 4; see Table 2 for complete individual results, means, and standard errors). Subjects also waited longer to approach on face-forward than face-back trials (Wilcoxon test, $Z = -2.666$, $P = 0.008$, $r = 0.54$). However, subjects’ preferences for the silent box did not differ from chance on any condition (Wilcoxon test, *noncompetitive*: $P = 0.67$; *back*: $P = 0.55$; *forward*: $P = 0.56$; Fig. 5). Additionally, subjects did not show a significant preference on the first face-back trial overall ($N = 9$, Wilcoxon test, $P = 0.096$), or on the first face-back trial for which they made a choice ($N = 10$, Wilcoxon test, $P = 0.058$). Specifically, on the first face-back trial, seven subjects approached the silent box and two approached the noisy box. Of the three subjects that made no approach on their first trial, one approached the silent box on her next face-back trial and two never made an approach. On face-forward trials, only six individuals ever made an approach: three approached the silent box and three approached the noisy box.

Discussion

Lemurs approached less, and more slowly, when the experimenter could see them, suggesting that they are sensitive to social information concerning the visual perception of others. Given that there was no alternative food option in the face-forward trials, and that there was no punishment for approaching, this result is particularly notable. Furthermore, this result suggests that lemurs understood the competitive nature of the task. However, lemurs had no preference for the silent box in the critical face-back condition when the experimenter could not see,

Table 2 Complete individual results for Experiment 2, including means and standard errors

Subject	Noncompetitive approach (%)	Face-forward approach (%)	Face-back approach (%)	Noncompetitive silent—first choice (%)	Face-forward silent (%)	Face-back silent (%)	Face-forward latency (s)	Face-back latency (s)	First face-back trial	First face-back approach	First face-forward approach
Schweppes	100	0	100	25	—	25	120	12.5	S	S	—
Ginger	100	0	50	37.5	—	100	120	63.5	—	S	—
Alena	50	0	75	100	—	66.7	120	38.2	S	S	—
Sprite	100	50	75	75	50	66.7	65	47	N	N	N
Rolfe	12.5	0	0	0	—	—	120	120	—	—	—
Johan	100	50	50	75	0	50	66.8	63	S	S	N
Fern	25	0	0	100	—	—	120	120	—	—	—
Berisades	100	25	100	37.5	100	50	92	10.5	S	S	S
Tellus	87.5	0	100	14.3	—	75	120	24	S	S	—
Edelweiss	100	50	100	85.7	50	75	95.8	5.2	S	S	N
Aracus	100	100	100	62.5	50	50	7.5	7.5	S	S	S
Sierra Mist	87.5	25	25	28.6	100	0	91.8	91	N	N	S
Mean	80.2	25.0	64.6	53.4	58.3	55.8	94.9	50.2	—	—	—
SE	9.3	9.2	11.3	9.8	10.9	8.1	10.0	12.1	—	—	—

All values are reported as percentages (of total trials) or seconds, except for the first trial and first approach columns, for which S = 'silent' and N = 'noisy'

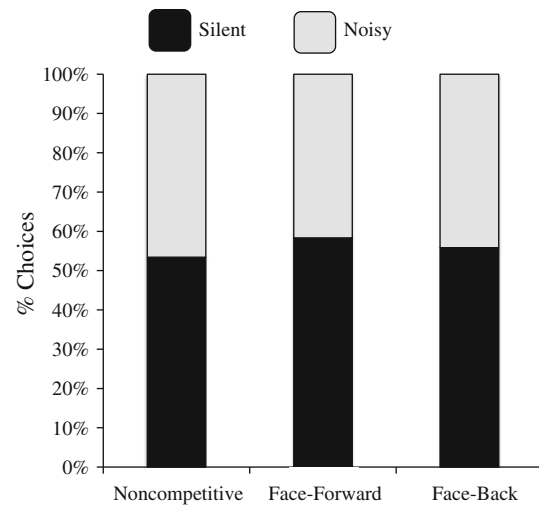


Fig. 5 Mean percentage of trials that subjects approached the silent and noisy boxes for each condition of Experiment 2 when a choice was made at all. Lemurs did not have significant preference for either box in any condition

suggesting that they are not sensitive to what others can hear. The first trial analysis of the face-back condition shows a weak trend toward approach of the silent box; however, this is unlikely to be a robust effect because subjects who demonstrated success in similar studies on both visual and auditory tasks performed consistently well across trials, not just on the first trial (Melis et al. 2006; Sandel et al. 2011; MacLean et al. 2013). Still, a larger sample like that in Santos et al. (2006) would be useful to confirm whether or not lemurs are behaving differently in the first trial compared to the session as a whole.

General discussion

Together, the results from both experiments suggest that the social-cognitive abilities of ring-tailed lemurs are inflexible and do not generalize across sensory domains. These data replicate previous studies demonstrating that lemurs are sensitive to being seen (Sandel et al. 2011; MacLean et al. 2013); however, our results suggest that lemurs are not responsive to being heard. This finding contrasts with studies of chimpanzees and rhesus macaques, both of whom have demonstrated success in very similar tasks, suggesting that the convergence between haplorhine primates and ring-tailed lemurs is limited to exploiting information about another's visual perception. It may also suggest that the cognitive mechanisms being utilized to exploit visual information differ between clades.

One explanation for these findings is that the cognitive requirements for understanding what another individual can see and hear are different. For example, choosing food that another individual cannot see, at minimum, requires

only a very simple egocentric rule, such as “avoid faces.” Thus, an individual might *exploit* social information about what another individual can see without *knowing* what she can see (i.e., without actually mentally representing her perspective). Within primates, perspective-taking abilities have only been found in monkeys and apes (Hare et al. 2000, 2001, 2006; Santos et al. 2006; Bräuer et al. 2007; Kaminski et al. 2008; Marticorena et al. 2011; Crockford et al. 2012; MacLean and Hare 2012). Thus, it may be that lemurs are using a very low-level mechanism to solve social competition problems. This hypothesis is supported by the finding that, unlike haplorhines, lemurs do not spontaneously follow the gaze of others (Tomasello et al. 1998; Sandel et al. 2011; but see Ruiz et al. 2009). Although gaze following alone is not indicative of perspective taking, the absence of even reflexive gaze following is suggestive of a similar absence of high-level social-cognitive mechanisms.

Other lines of evidence also support this hypothesis. For example, in the study by MacLean et al. (2013), although lemurs ultimately avoided stealing from experimenters “who could see them,” they sometimes initially approached the “seeing” experimenter and only as they got closer—as the social cue associated with seeing, the face, became more salient—did they stop, turn around, and make the “correct” choice (personal observations). This pattern of behavior is indicative of responding specifically to the social cue and not the mental state of the experimenter. In the present study, however, such social cues did not exist. Instead, to succeed, lemurs were required to attend to the noise-producing capabilities of each box and understand that choosing the noisy option would alert the human competitor. The lemurs’ failure on the task, thus, likely owes to the absence of persistent social cues and, ultimately, to an inability to mentally represent the perceptually relevant qualities of the apparatus or the mental states of the experimenters.

To further elucidate the cognitive mechanisms being used by lemurs to exploit visual information, future studies should employ methods that make divergent predictions depending on whether subjects are exploiting social cues or representing mental states. For example, Hare et al. (2001) found that subordinate chimpanzees approached food more often when competing against ignorant dominants that lacked accurate information about the location of food than when competing against knowledgeable dominants. Subordinates were required to make a decision before the dominant individual entered the testing room, suggesting that they were responding to their competitor’s mental state (in this example, knowledge or ignorance about the location of food) rather than to social or behavioral cues. Moreover, multiple studies suggest that chimpanzees exploit a human competitor’s visual perspective even when they cannot see the competitor while making their decision (e.g., Hare et al.

2006; Melis et al. 2006). In addition to investigating whether lemurs can succeed on visual tasks in the absence of visible social cues like faces, it would be informative to integrate social cues into the methods of auditory tasks to determine whether lemurs can apply similar low-level rules to exploit what a competitor can and cannot hear, or whether their adaptive responses to social cues associated with perception are unique to the visual domain.

It is nonetheless possible that the design of the study was not ecologically meaningful, and that this accounts for why the lemurs did not succeed. However, as mentioned previously, other species have shown success in similar experiments (Melis et al. 2006; Santos et al. 2006), and ring-tailed lemurs themselves have shown success on studies in the visual domain (Sandel et al. 2011; MacLean et al. 2013). Numerous studies in recent years have also validated the competitive paradigm (Hare et al. 2000, 2001, 2006; Hare and Tomasello 2004; Flombaum and Santos 2005; Melis et al. 2006; Santos et al. 2006; Bräuer et al. 2007; Kaminski et al. 2008). Thus, ecological factors do not appear to explain our findings, though smaller design choices could theoretically have influenced the results. For example, the task in Experiment 2 was not identical to Santos et al. (2006), on which it is based. Changes were made to accommodate differences in typical lemur behavior (a front flap instead of hinged top on the food box) and the relatively few subjects available to test (many trials per subject instead of just one, requiring the location of the noisy and silent boxes to shift between blocks).

This is the first study to explore auditory perspective taking in lemurs, and future studies may find novel ways to address this question. Unlike reports from anthropoid primates (Crockford et al. 2012; Hauser 1992), it may be that lemurs are not under significant pressure to exploit the auditory perception of conspecifics. Playback studies requiring less attention on the part of the lemurs might be more successful in teasing apart how lemurs use auditory information in social contexts. It will also be interesting to consider lemur perspective taking in other sensory modalities (e.g., olfaction: Scordato and Drea 2007). Finally, in species that do attend to multiple perceptual channels, an avenue for further research is how these species integrate and prioritize knowledge of others’ sensory information across domains, especially when these channels of information conflict.

Overall, the results of the present study emphasize the importance of experimentally investigating social cognition across sensory domains in order to shed light on the ultimate selective forces and cognitive mechanisms necessary for apparently complex social behavior. The results provide evidence for the hypothesis that social complexity as defined by group size is not sufficient for social-cognitive abilities that require sophisticated underlying

mechanisms. This research suggests that the social dynamics of haplorhine groups impose greater cognitive demands than those of ring-tailed lemurs.

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Ethical standards Ethical approval was given by the Duke University Institutional Animal Care and Use Committee (Protocol #: A199-11-08) and veterinarians at the Duke Lemur Center.

Conflict of interest The authors declare that they have no conflict of interest.

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