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Social inhibitory control in five lemur species

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Abstract We tested five lemur species—ring-tailed lemurs, ruffed lemurs, mongoose lemurs, black lemurs, and Coquerel's sifakas—($N = 52$) in an experiment that evaluated skills for inhibitory control in a social context. First, two human experimenters presented identical food rewards; the "generous" experimenter allowed the subject to eat from her hand, whereas the "competitive" experimenter always withheld the reward. Lemurs quickly learned to approach the generous experimenter and avoid the competitive one. In the inhibition test phase, we endowed the competitive experimenter with a more valuable food reward but the competitive experimenter continued to withhold food from the subject. Thus, lemurs were required to inhibit approaching the more desirable reward in favor of the lesser but obtainable reward presented by the generous experimenter. In test trials, lemurs' tendency to approach the competitive experimenter increased from the reputation phase, demonstrating sensitivity to the experimental manipulation. However, subjects approached the larger reward less frequently in test trials compared with pretest food-preference trials, evidencing some capacity for inhibitory control in this context. Despite differences in sociality and ecology, the five lemur species did not differ in this ability. Although the study did not uncover species differences, this experimental task may provide a useful measure of social inhibition in broader comparative studies.

Keywords Strepsirrhines · Cognitive evolution · Inhibition · Lemur cognition

Introduction

When exposed to the myriad stimuli of their natural environments, animals must inhibit some behavioral responses in favor of others. In this vein, diverse input can present a conflict to an individual who must distinguish which choice is the most effective (Hinde 1970). For example, a squirrel enjoying an acorn must cease feeding and run for cover when a predator flies overhead; a chimpanzee may benefit by refraining from eating a fruit before it ripens. Such inhibitory control underlies many cognitive faculties and is likely important in most decisions related to survival and reproduction. The importance of inhibition also manifests itself in the modern lives of humans. For example, choosing to wait longer for a larger reward is linked to financial and academic success later in life (Mischel et al. 1989). What are the selective factors that favor inhibitory control? To address this question, a comparative approach is needed (MacLean et al. 2012, 2014).

Inhibitory control—the ability to choose an effective response over a tempting or distracting but ineffective one—has been studied in a wide array of species and through numerous experimental paradigms (e.g., apes: Vlamings et al. 2006; Dufour et al. 2007; Hayden and Platt 2007; Rosati et al. 2007; Uher and Call 2008; Beran and Evans 2009; Vlamings et al. 2010; Stevens et al. 2011; New World monkeys: Santos et al. 1999; Stevens et al. 2005a, b; Anderson et al. 2010; Pelé et al. 2011; Paglieri

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et al. 2013; Old World monkeys: Evans and Beran 2007; Pelé et al. 2010, 2011; lemurs: Genty et al. 2004, 2011; Genty and Roeder 2007; Stevens and Mühlhoff, 2012; MacLean et al. 2013; African grey parrots: Vick et al. 2010; cockatoos: Auersperg et al. 2013; sparrows: Boogert et al. 2011; and dogs: Bray et al. 2014a, b). Most recently, a large-scale phylogenetic comparison of inhibitory control in 36 species revealed species differences that were strongly correlated with absolute brain volume and dietary complexity in primates (MacLean et al. 2014).

However, the paradigms used to assess inhibitory control as well as definitions of this construct vary widely. In many cases, diverse measures of inhibitory control converge with one another, suggesting a coherent cognitive construct with the potential to explain individual or species differences in a variety of behavioral domains (Duckworth and Kern 2011; Moffitt et al. 2011). However, other studies suggest that inhibitory control is also influenced by the decision-making context, and an individual's (or species') ability to resist prepotent responses may be highly context specific (Tsukayama et al. 2012; Bray et al. 2014a, b). Thus, it is important that comparative studies of inhibitory control investigate these processes in a wide range of problem-solving contexts. This study builds on previous research on lemur inhibitory control when solving physical problems (MacLean et al. 2013) by investigating these abilities in a social context.

Social inhibition requires resisting one behavioral response in favor of another as a result of a social factor (e.g., Wobber et al. 2010). For example, animals may behave differently in the presence of particular group mates based on their relationships with these individuals. This flexibility may be facilitated by forming reputations about group mates, or "judgments [that] involve the attribution of stable character traits or behavioral dispositions to specific individuals in a flexible and adaptive manner" (Subiaul et al. 2008). Based on this knowledge, individuals can flexibly express or inhibit certain behaviors depending on the social context. For instance, a low-ranking animal may benefit by inhibiting the desire to feed or mate in the presence of a high-ranking animal, where these behaviors may be freely expressed in other contexts. This type of social inhibition may draw on general cognitive resources for self-control, or alternatively, specialized skills for social inhibition may evolve independently in response to social-selection pressures.

Evidence for a distinctly social form of inhibitory control is suggested by research on nonhuman apes (Wobber and Hare 2009). In a reversal-learning paradigm, chimpanzees rapidly switch from begging from a human who was "generous" to one who was "competitive" within one or two trials of the humans reversing roles. The same chimpanzees showed more typical, slow reversal speed in a more standard nonsocial reversal task (Wobber and Hare 2009; Wobber et al. 2014). In other nonsocial measures of inhibitory control, chimpanzees and their closest relatives, bonobos, do not differ in performance (Vlamings et al. 2006), but a direct quantitative comparison between the species on two measures of social inhibition found that bonobos showed delayed development in inhibitory control as well as less social inhibition overall compared with age-matched chimpanzees (Wobber et al. 2010, 2014). These studies indicate that inhibitory control is employed differently in social and nonsocial contexts and that animals may perform better on social tests of inhibition compared with nonsocial inhibitory control tasks, such as the classic reverse-contingency task.

To understand the adaptive function of social inhibition more broadly, further comparisons are needed. Studying the performance of multiple, closely related species that differ in their sociality and ecology is one promising approach for understanding how and why inhibitory control capabilities may have evolved (MacLean et al. 2012). We tested five lemur species that vary in their feeding ecologies and social systems in a social inhibition task. Ring-tailed lemurs (*Lemur catta*) are dietary generalists and form large, hierarchal social groups similar to those of Old World monkeys (Jolly 1966; Sauther et al. 1999). Ruffed lemurs (*Varecia variegata variegata*, *V. v. rubra*) are highly frugivorous and spend most of their time in association with a small group of kin that fission–fusion within a larger community (Britt 2000; Vasey 2007a). Coquerel's sifaka (*Propithecus coquereli*) are folivorous and form medium-sized multi-male—multifemale groups (Richard 1978). Black lemurs (*Eulemur macaco macaco, E. m. flavifrons*) and mongoose lemurs (*E. mongoz*), are frugivore–folivores, with diets that shift seasonally from fruit to flowers, leaves, and nectar, and they typically reside in medium-sized groups and pair bonds, respectively (Colquhoun 1998; Curtis 2004). If species differences in inhibitory control are evolutionarily linked to social systems (Amici et al. 2008), we predicted that lemur species living in large or complex social groups (ring-tailed lemurs and ruffed lemurs) would perform best on these tasks. Alternatively, if species differences in inhibitory control are linked to dietary strategies (Stevens et al. 2005a, b; Rosati et al. 2007), we predicted that the most frugivorous species (ruffed lemurs) would perform best and that the most folivorous species (Coquerel's sifakas) would perform worst in this context.

Methods

All research reported in this manuscript was noninvasive and adhered to protocols approved by Duke University's Institutional Animal Care and Use Committee and the legal requirements of the USA.

Subjects

We tested 52 subjects representing five lemur species: ten ring-tailed lemurs, 12 mongoose lemurs, ten ruffed lemurs, ten black lemurs, and ten Coquerel's sifakas. Details regarding subjects' age, sex, and experiment participation are shown in Table 1.

All lemurs were housed at the Duke Lemur Center. Lemurs lived in pairs or groups and occupied indoor rooms and outdoor semi-free-ranging enclosures. We tested subjects in a room in their home enclosure while separated from all other group members. Food was temporarily removed during the experimental sessions, but water was available ad libitum. All trials were recorded using a JVC Everio camcorder.

Table 1 Names, ages, sexes, and experiment participation of lemur subjects

Species	Subject	Age (years)	Sex	Detour-reaching	Social inhibition
Lemur catta	Cap N'Lee	8.2	M	×	×
	Nemo	20.9	M	×	
	Cleonomis	20.8	F	×	
	Tellus	4.1	F	×	
	Ginger	2.2	F	×	
	Teres	13.1	M	×	
	Nicaea	5.4	F	×	
	Berisades	5.4	M	×	×
	Cleis	24.1	F	×	×
	Lilah	4.4	F	×	×
	Ivy	3.1	M	×	
	Licinius	16.0	M		×
	Fritz	6.4	M		×
	Dory	19.5	F		×
	Aracus	17.9	M		×
	Aristides	14.1	M		×
	Sosiphanes	12.1	F		×
Eulemur mongoz	Concepcion	23.3	F	×	×
	Moheli	20.8	F	×	
	Eduardo	14.9	M	×	
	Paco	10.8	M	×	×
	Mercedes	4.1	M	×	
	Piedad	21.8	F	×	×
	Julio	19.3	M	×	×
	Maddie	3.3	F	×	×
	Sancho	26.7	M	×	×
	Flor	23.1	F	×	×
	Pedro	18.2	M		×
	Jorge	20.9	M		×
	Selena	11.9	F		×
	Guadalupe	14.0	F		×
	Fabio	20.9	M		×
Varecia variegata	Alphard	18.9	M	×	
	Borealis	19.9	M	×	
	Antlia	18.9	F	×	×
	Carina	4.1	F	×	×
	Aries	0.9	M	×	×
	Little dipper	5.9	F	×	
	Junior	4.4	M	×	×
	Comet	24.0	M	×	×

Table 1 continued

Species	Subject	Age (years)	Sex	Detour-reaching	Social inhibition
	Grace	12.3	F	×	×
	Diphda	19.2	F	×	×
	Hunter	11.8	M	×	
	Hebe	17.7	F		×
	Avior	0.8	M		×
	Minias	15.0	M		×
Eulemur macaco	Barrymore	19.8	M	×	×
	L'amour	17.7	F	×	×
	Foster	12.1	F	×	
	Olivier	17.0	M	×	×
	Harlow	15.9	F	×	×
	Quinn	7.2	M	×	
	Tarantino	9.0	M	×	
	Redford	17.2	M	×	×
	Teucer	20.2	M	×	×
	Hesperus	25.2	M	×	×
	Hopkins	13.1	M		×
	Deucalion	20.1	M		×
	Harmonia	24.7	F		×
Propithecus coquereli	Gordian	12.4	M	×	×
	Anastasia	4.3	F	×	×
	Pia	9.2	F	×	×
	Antonia	10.2	F	×	×
	Gratian	6.1	M	×	
	Jovian	4.2	M	×	×
	Tiberius	21.4	M	×	
	Matilda	1.7	F	×	×
	Lucius	3.4	M	×	×
	Marcus	5.6	M	×	×
	Maximus	5.2	M		×
	Irene	2.6	F		×

Procedure

We adapted a social inhibitory control task previously used with domestic dogs (Bray et al. 2014a, b). Subjects were presented with two humans holding an identical food reward. One human allowed the lemur to feed freely ("generous" experimenter), whereas the other human removed the food before the lemur was able to feed ("competitive" experimenter). Halfway through the session, the competitive experimenter began to present a larger array of food, while the generous experimenter continued to hold the small food reward. Thus, lemurs were initially required to learn to inhibit approaching the competitive experimenter and then to maintain this strategy in the face of novel task demands (i.e., when the competitive experimenter presented a higher value, but still unobtainable reward). Thus, the test trials in this paradigm are similar to those from the reverse contingency task that has been used with a variety of species (e.g., Boysen and Berntson 1995; Silberberg and Fujita 1996; Anderson et al. 2004; Genty et al. 2004, 2011; Kralik 2005; Murray et al. 2005; Vlamings et al. 2006; Albiach-Serrano et al. 2007; Chudasama et al. 2007; Genty and Roeder 2007; Uher and Call 2008; Danisman et al. 2010). The main difference between previous methods and our study methodology is that our task incorporates human social agents as the discriminative stimuli, rather than inanimate objects. While social discrimination rules often take animals hundreds of trials to learn (Tomasello and Call 1997), social rules can be learned quickly (Hare 2001). Previous studies indicate lemurs regard humans as social agents and flexibly adjust their behavior in response to human social cues (Sandel et al. 2011; MacLean et al. 2013; Bray et al. 2014a, b). Thus, the challenge with which we presented our lemur subjects was a social one, although additional spatial cues may have facilitated this discrimination (see below).

Value discrimination

To test lemurs' ability to discriminate between a greater and lesser quantity and quality of food, subjects first participated in a value discrimination pretest (20 trials). An experimenter presented the subject with a display of food in each hand. The low-value option consisted of one grape piece. The high-value option consisted of four grape pieces, one banana piece, and one raisin (Fig. 1). Due to dietary differences, the rewards used for sifakas were one walnut piece in the low-value display, and four walnut pieces, two almond pieces, and one peanut in the high-value display. Before each trial, the subject was attracted (with food) to a stationing location 1 m in front of the experimenter. The experimenter then presented the subject with the two displays side by side, and once the subject oriented toward the experimenter, the experimenter moved her hands 0.5 m apart and faced downward to avoid unintentionally cuing the lemur to one side. The subject was then allowed to approach and feed from one hand. Once the subject had approached one of the experimenter's hands, operationally defined as the lemur's hand or snout crossing the threshold of the hand, the experimenter allowed the subject to feed for 2 s and closed her other hand, making its contents inaccessible. Throughout the session, the side with the high-value reward (left or right) was the same within subjects but counterbalanced between subjects, a spatial cue that may have facilitated the discrimination. Subjects were required to approach the larger amount of food on 14/20 (for which $p = 0.0576$ in a one-tailed test where we predict that lemurs will prefer the larger amount of food) trials to move on to the test session. If subjects did not approach the stationing location within 10 min or exhibited signs of stress (e.g., pacing, excessive scent marking, refusal to eat food), the session was aborted (14 sessions). If subjects had completed at least 15 trials of the aborted session, data were included for analysis (three subjects, all of whom chose the large quantity on 100 % of trials before the session was aborted, thus meeting the 14/20 criterion). Otherwise, subjects were eligible to participate in another value discrimination test at a later time. Subjects that did not choose the larger quantity of food on 14/20 trials were also eligible to be retested at a later time.

Test

We conducted test sessions at least one day after value discrimination sessions. The test consisted of two phases: a direct reputation phase (10 trials) and, immediately following, an inhibitory control phase (10 trials). In the reputation phase, two experimenters (neither of whom administered the value discrimination pretest) presented the subject with equal amounts of food. The "generous" experimenter allowed the subject to feed from her hand, while the "competitive" experimenter did not. Consistent with previous studies involving a reputation component (e.g., Subiaul et al. 2008; Herrmann et al. 2013; Bray et al. 2014a, b), we use the terms generous and competitive as

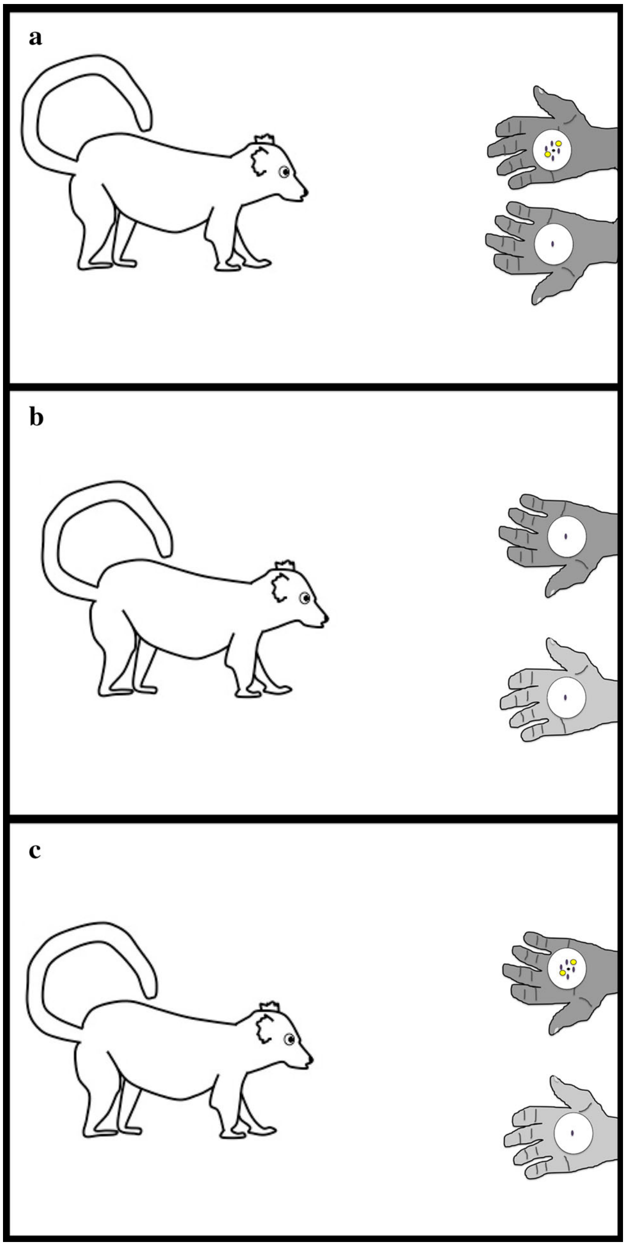

Fig. 1 Experimental setup of the social inhibition task,showing **a** the value discrimination pretest with a single experimenter, **b** the reputation phase of the test with two new experimenters, and **c** the inhibition phase of the test, with the same two experimenters

descriptive labels for the behavioral roles of the human experimenters. As in the pretest, the subject was first attracted to the stationing location with a food reward. Both experimenters, positioned equidistant to the subject, displayed one food piece in one hand (1 grape piece, or 1 walnut piece for sifakas). Experimenters held their hands side by side until the subject oriented toward them. They then simultaneously moved their hands 0.5 m apart, faced downward, and the subject was allowed to approach (Fig. 1). The identity of the experimenters, the roles that they played, and the side on which they sat, were counterbalanced between subjects (Fig. 1). Counterbalancing sites within subjects was not logistically feasible; in pilot studies, this amount of movement by experimenters precluded our ability to complete test sessions with lemurs. We ensured that all subjects interacted with both experimenters. Subjects may have used the side on which the experimenter sat (left or right) to learn which food to approach and avoid, but given lemurs' ability to respond to humans as competitive agents (Sandel et al. 2011; MacLean et al. 2013; Bray et al. 2014a, b), we doubt that the lemurs discriminated between food options solely based on the side. Thus, the experimental design retains the desired effect of providing a social cue for the lemurs.

If the subject approached the generous experimenter, it was allowed to consume the food in her hand, and the competitive experimenter removed her hand. If the subject approached the competitive experimenter, the competitive experimenter removed her hand immediately, and the subject was given 3 min to approach and eat the food offered by the generous experimenter. This procedure ensured that the generous experimenter always acted "generously" and never took food away form an approaching subject, but only the lemur's first approach was considered when scoring choice behavior, allowing comparison against chance expectation (50 %). If the subject did not approach the generous experimenter within this 3-min period, the next trial was administered. During the ten reputation trials, subjects were required to approach both the competitive and generous experimenters at least one time. We implemented this criterion so that all subjects had experience approaching both experimenters before advancing to the inhibition phase of the task. If subjects did not meet this criterion, the full test session could be repeated at a later date (two subjects). If subjects met the criterion, they proceeded immediately to the inhibition phase.

In the inhibition phase, the procedure was identical, except that the competitive experimenter displayed the high-value reward (identical to the high-value reward from the value discrimination), while the generous experimenter continued to present a single piece of food (Fig. 1). If a subject approached the generous experimenter, she allowed the subject to feed from her hand. If a subject approached the competitive experimenter, she withdrew her hand and did not allow the subject to feed. As in reputation trials, the subject was then allowed 3 min to approach and feed from the generous experimenter's hand. We allowed subjects to self-correct in this manner to encourage continued participation in the experiment. If the subject did not approach the generous experimenter within 3 min, the next trial was administered. Subjects were thus required to inhibit approaching a desirable but unobtainable food reward in favor of a less desirable but obtainable reward. As in the pretest session, if a subject did not approach the stationing location within 10 min or exhibited signs of stress, the session was aborted and could be repeated at a later time (eight sessions).

Analysis

All sessions were filmed, and a second observer coded 20 % of all trials from video. Interrater reliability was almost perfect (Cohen's kappa = 0.96, Altman 1991). Therefore, scores from the live coding were used for all analyses. Data were analyzed using IBM SPSS Statistics Version 20. We used nonparametric analyses and report the standardized test statistic throughout. For post hoc comparisons, we reported the adjusted p value, which allows interpretation against the traditional 0.05 threshold after compensating for multiple pairwise comparisons (Hochberg and Benjamini 1990). For all tests with a directional prediction, we used a directional hypothesis-testing framework following the conventions ($\delta = 0.01$, $Y = 0.04$) recommended by Rice and Gaines (1994). Accordingly, the null hypothesis was rejected when the one-tailed p value was ≤ 0.04 in the predicted direction, or ≥ 0.99 in the unanticipated direction. For all directional predictions, we report the one-tailed p value. Following ar the predictions:

1. In the value discrimination pretest, subjects were expected to prefer the array with the greater quality and quantity of food.
2. If subjects were capable of discriminating between experimenters based on their behavior, we expected subjects to choose the competitive experimenter less frequently in the second compared with the first half of reputation trials.
3. Similarly, we predicted that lemurs would approach the competitive experimenter less often than expected by chance in the second half of reputation trials.
4. When the inhibitory control phase began, we expected lemurs to initially increase their choices to the competitive experimenter, who presented the preferred reward.
5. However, if subjects were capable of (partially) inhibiting their approaches to the desired reward, we

expected them to choose it less frequently in test trials than in the initial value discrimination.

Results

Value discrimination

On average, lemurs met the criterion of choosing the larger quantity of food at least 14/20 times in a single session (mean number of sessions to criterion = 1.1 ± 0.1), and the number of value discrimination sessions required did not differ between species (Kruskal–Wallis test: $H_4 = 3.28$, $P = 0.51$). Lemurs approached the high-value food on 92 ± 1 % of trials, significantly more often than expected by chance (one-sample Wilcoxon test: $T = 6.33$, $N = 52$, $P < 0.01$), and species did not differ on this measure (Kruskal–Wallis test: $H_4 = 9.10$, $P = 0.06$).

Reputation phase

Pooling all species, lemurs learned to avoid the competitive experimenter in the reputation phase. They approached the competitive experimenter significantly less often in the second half (mean = 39 ± 3 %) than in the first half (mean = 52 ± 4 %) of reputation trials (Wilcoxon test: $T = -2.69$, $N = 52$, $P < 0.01$). Importantly, in the second half of the reputation phase, lemurs approached the competitive experimenter less often than expected by chance (one-sample Wilcoxon test: $T = -3.05$, $N = 52$, P <0 .01; Fig. 2). A direct comparison of the five species on the second half of reputation trials revealed no significant species differences (Kruskal–Wallis test: $H_4 = 5.65$, $P = 0.23$). One-sample Wilcoxon tests for each species revealed that mongoose lemurs, ring-tailed lemurs, and ruffed lemurs showed a significant preference for the generous experimenter in the second half of the reputation phase but that black lemurs and sifakas did not differ from chance expectation (Table 2).

Inhibition phase

Overall, lemurs approached the high-value food, held by the competitive experimenter, on the majority of inhibition trials (one-sample Wilcoxon test: mean = 60 ± 3 %, $T = 2.52$, $N = 52$, $P = 0.01$). However, they did so significantly less often during this phase, after exposure to the competitive vs. generous experimenters, than during the value discrimination phase, which measured their initial food preferences (Wilcoxon test: mean = 92 ± 1.1 % of trials, $T = -5.78$, $N = 52$, $P < 0.01$; Fig. 3). All species exhibited some degree of inhibitory control, approaching the high-value reward significantly less often in the inhibition phase than in the value discrimination phase (Table 2).

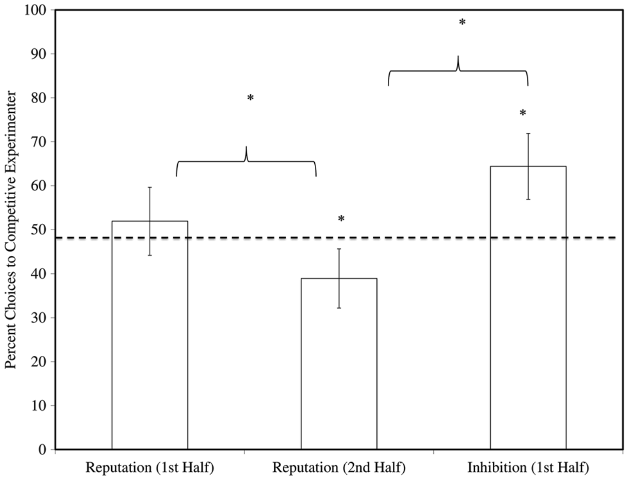

Fig. 2 The percentage of trials in which lemurs chose the competitive experimenter during the first and second halves of the reputation phase and the first half of the inhibition phase. Lemurs learned to avoid the competitive experimenter during the reputation trials. However, subjects approached the competitive experimenter again during the inhibitory-control trials, when she offered a larger (but still unobtainable) reward. *Asterisks* over *brackets* indicate significantly different pairs of means. *Asterisks* over *vertical bars* indicate significant deviation from chance. *Error bars* reflect 95 % confidence intervals

We then examined differences in species' capabilities for inhibitory control. To account for subjects' individual preferences for the high-value reward, we assessed relative levels of inhibitory control by generating a difference score for each subject. This difference score was calculated as the percent of trials in which subjects approached the high-value reward in the value discrimination phase (when it was obtainable), minus the percent of trials in which subjects approached the high-value reward during the inhibition phase (when it was unobtainable). Thus, a larger difference score corresponds to a greater degree of inhibitory control. Although the mean difference scores ranged widely between species (range 18–45), a direct comparison of these scores revealed no species differences (Kruskal–Wallis test: $H_4 = 7.56$, $P = 0.11$). Therefore, species exhibited similar levels of inhibitory control after we controlled for differences in performance during the value discrimination.

Although lemurs successfully avoided the competitive experimenter in the second half of the reputation phase (mean choices to competitive experimenter 39 ± 3 %), their tendency to approach the competitive experimenter rebounded in the inhibition phase when the high-value reward was presented (Fig. 2). This was true for lemurs overall (mean choices to competitive experimenter 64 ± 4 %; Wilcoxon test: $T = 4.72$, $N = 52$, $P < 0.01$)

Table 2 Species-specific results

Species	N	Choices to competitive experimenter during second half of reputation phase compared with chance (%)			Choices to larger array of food during value discrimination compared with inhibiton phase (%)				Choices to competitive experimenter during first half of inhibition phase compared with second half of reputation phase		
		Mean ± SD	Wilcoxon T	p	Mean ± SD (value discrimination)	Mean ± SD (inhibition phase)	Wilcoxon T	p	Mean ± SD	Wilcoxon T	p
Mongoose lemur	12	35 ± 21.1	−2.08	0.02	95 ± 6.4	50.3 ± 23.5	−3.06	<0.01	48.3 ± 30.1	1.63	0.05
Ring-tailed lemur	10	28.5 ± 23.3	−2.23	0.01	96 ± 5.2	65 ± 29.1	−2.81	<0.01	64 ± 33.7	2.1	0.02
Ruffed lemur	10	36 ± 20.7	−1.84	0.03	85 ± 10.8	47 ± 17.7	−2.71	<0.01	56 ± 15.8	1.89	0.03
Black lemur	10	54 ± 23.2	0.32	0.38	94 ± 6.1	66 ± 21.2	−2.53	0.01	72 ± 27.0	1.98	0.03
Sifaka	10	42 ± 31.9	−0.83	0.2	91 ± 7.0	73 ± 26.7	−1.78	0.04	84 ± 15.8	2.55	<0.01

SD standard deviation

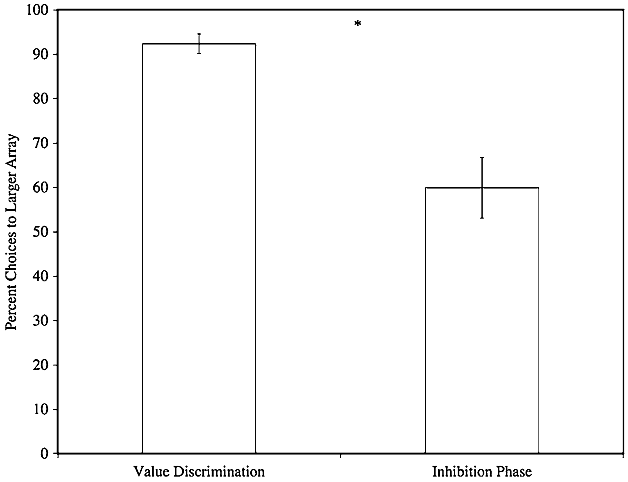

Fig. 3 Overall results from the social inhibition task. Lemurs inhibit approaching the larger array of food, approaching it on fewer trials in the inhibition phase than during the value discrimination. *Asterisks* indicate significantly different pairs of means. *Error bars* reflect 95 % confidence intervals

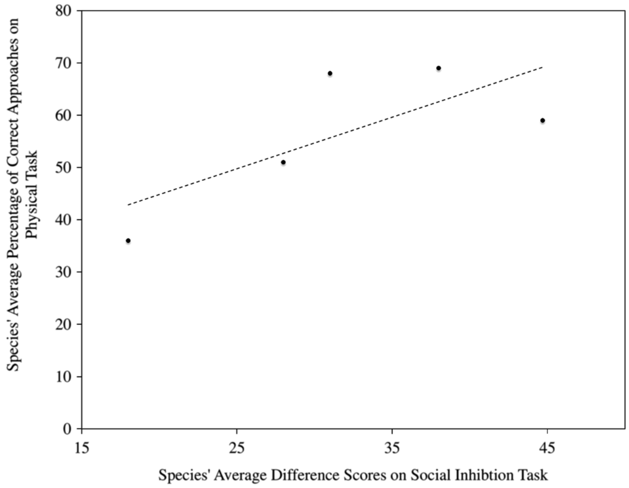

Fig. 4 Correlations of species means between the social inhibition experiment (species' average difference scores) and the detour-reaching experiment (species average percent "correct" approaches). The slope is positive but not statistically significant ($r_s = 0.70$, $N = 5$, $P = 0.19$)

and for each species individually (Table 2). These results indicate that lemurs were sensitive to the experimental manipulation and were initially unable to continue avoiding the competitive experimenter, as they had done during the reputation phase.

To test whether performance was related to a subject's age, we assessed the correlation between age and the difference score described above. Inhibitory control was not correlated with age in the social inhibition task ($r_s = 0.19$, $N = 52$, $P = 0.19$). To explore the possibility of sex differences, we compared difference scores between the sexes across species. This analysis revealed no significant sex differences, but males trended toward outperforming females, and the male mean was higher than the female mean in all species (male mean = 38 ± 4, female mean = 24 ± 5; Mann–Whitney $U = 1.78$, $N = 52$, $P = 0.08$).

Lastly, to explore whether performance in this social inhibitory control task was correlated with performance on a nonsocial inhibitory control task, we compared these data to data from a previously published study of inhibitory control assessing the same species and many of the same subjects (MacLean et al. 2013). For this analysis, we used the difference score (described above) as the primary measure of inhibitory control for the social task. To assess this question at the individual level, we fit a linear model with species and scores on the physical inhibitory control task as predictors of the difference score from the social inhibitory control task. Controlling for species, scores on the physical inhibitory control task did not predict performance on the social task ($t_{27} = 0.68$, $P = 0.50$). At the species levels, scores on the two tasks covaried positively but not significantly ($r = 0.70$, $N = 5$, $P = 0.19$; Fig. 4).

Discussion

After a brief encounter, lemurs made direct reputation-like judgments about two human experimenters. They maintained these reputation-like judgments when faced with a conflict of interest by successfully inhibiting their approach toward a desired food reward when the uncooperative human possessed it. In all phases of the experiment, lemurs showed sensitivity to the experimental manipulations. During the initial value discrimination, all lemurs preferred the larger, more diverse array of food. In the reputation phase that followed, lemurs approached the competitive experimenter significantly less often in the second half than in the first half of the trials, showing that lemurs understood the choice contingencies in this context and were able to make reputation-like judgments. Then, during the inhibition phase, when the competitive experimenter presented the more desirable food array, lemurs initially had a tendency to resume approaching this individual, doing so more often in the first half of inhibition trials than they had in the last half of reputation trials. Although lemurs still approached the competitive experimenter on the majority of trials in the inhibition phase, they did so less often than they had during the value discrimination phase, when the desired food was obtainable. Therefore, these data suggest that lemurs were partially, but not completely, able to inhibit maladaptive behaviors in this social context. Despite differences in sociality and ecology, the five lemur species did not differ in this ability.

Our results align well with evidence from studies that show lemurs are more likely to choose a baited bowl when a cooperative rather than competitive experimenter is present (Genty and Roeder 2006; Genty et al. 2008). In contrast to our design, however, lemurs in previous studies learned the identities of human experimenters separately and through extensive training (Genty and Roeder 2006; Genty et al. 2008). During training, a cooperative experimenter gave the lemur a raisin when the lemur reached toward a baited bowl, and a competitive experimenter took the raisin away and pretended to eat it herself. After at least 200 trials with each experimenter, lemurs were more likely to indicate the baited bowl if the cooperative experimenter was present than if the competitive experimenter was present (Genty and Roeder 2006; Genty et al. 2008).

Thus, the rapidity with which lemurs in our study learned to distinguish between the generous and competitive experimenter is notable and reveals an important insight into study design. As in this study, Sandel et al. (2011) found that four species of lemurs learned within six trials to prefer approaching an isolated piece of food over one near a human competitor who would steal the food if the lemur approached. One species subsequently avoided food near a human face in favor of food near a human facing away (Sandel et al. 2011; Bray et al. 2014a, b), and in further studies, brown lemurs, black lemurs, and sifakas also demonstrated this ability (MacLean et al. 2013). This suggests that in contrast to their performance in a go—no-go task (e.g., Genty and Roeder 2006; Genty et al. 2008), lemurs can learn quickly and demonstrate a level of inhibition when making choices between two social options within a single session. Our present study and previous work with lemurs (Sandel et al. 2011; MacLean et al. 2013) emphasize the importance of measuring animals' cognitive abilities in an ecologically relevant context, for example, by simulating a social and competitive encounter (Hare 2001).

It is possible that lemurs did not form reputations in our experiment but, rather, learned a simple social rule that allowed them to distinguish between experimenters. However, this seems unlikely, as such discrimination learning typically takes a range of primate species hundreds of trials to master (Tomasello and Call 1997), and in our experiment, lemurs showed preference for the generous experimenter within ten trials. Thus, while spatial cues may also have facilitated learning in these studies, it is likely that the inclusion of both spatial and social cues allowed subjects to acquire the relevant discrimination with such rapidity.

As several lines of evidence suggest possible evolutionary links between diet, sociality, and inhibitory control (Amici et al. 2008; MacLean et al. 2014), it is surprising that there were no species differences in our sample, which represented a diversity of social systems and dietary patterns. For example, ring-tailed lemurs live in the largest groups, which are despotic and hierarchical; ruffed lemurs have been reported to exhibit fission–fusion social dynamics (Sauther et al. 1999; Gould 2007; Vasey 2007b). Both characteristics have been implicated in studies of flexible cognition in birds and primates (fission–fusion dynamics: Amici et al. 2008; sociality generally: Bond et al. 2007; Pelé et al. 2011; Sandel et al. 2011; MacLean et al. 2013; despotic social systems: Wobber et al. 2010).

However, it is important to note that the fission–fusion dynamics of ruffed lemurs are different from those of spider monkeys and chimpanzees, tested by Amici et al. (2008) and may involve less complex social interactions (Baden et al. 2013). Furthermore, several studies that, like ours, compare closely related species in inhibitory control capabilities find few species differences (among great apes: Vlamings et al. 2006; among ruffed and black lemurs: Stevens and Mühlhoff 2012). In contrast, ecological and neuroanatomical differences between species are more strongly related to species differences in inhibitory control in broader phylogenetic comparisons (MacLean et al. 2014).

Still, as ring-tailed lemurs do outperform less social species in other social paradigms (MacLean et al. 2008; Sandel et al. 2011; MacLean et al. 2013), it is surprising that they did not do so here. It is possible that because our task presented a choice between two food rewards of differing value that cognitive skills related less to sociality and more to foraging were demanded . Thus, species with challenging foraging demands, such as frugivores, might have better inhibitory control in this context than other closely related species (Rosati et al. 2007; Rosati and Hare 2013). Many studies have shown evidence for a relationship between foraging demands and inhibitory control. In a delayed-reward experiment, common marmosets, who eat gum that slowly flows from under bark, waited longer than cotton-top tamarins, who quickly catch flying insects, for a larger reward (Stevens et al. 2005a). A slight alteration of the paradigm revealed further differences reflective of foraging: tamarins, which move long distances to feed on insects, traveled farther than marmosets to acquire a larger food reward (Stevens et al. 2005b). A similar phenomenon was shown in apes: chimpanzees, whose food tends to be more patchily distributed than that of bonobos (Malenky and Wrangham 1994), waited longer than bonobos for a desired food reward (Rosati et al. 2007; Rosati and Hare 2013). Similarly, omnivorous rhesus macaques could not wait as long for a reward as frugivorous chimpanzees tested in other experiments (Evans and Beran 2007).

Ruffed lemurs were the only true frugivores in our sample and are in fact the only highly frugivorous lemur species (Vasey 2007b). Thus, it was difficult for us to isolate differences in diet and sociality among our study species, a problem also faced by Amici et al. (2008). Still, the social hypothesis predicts that both ruffed lemurs and ring-tailed lemurs should outperform other species, while the feeding ecology hypothesis predicts that ruffed lemurs should perform best (as they do in spatial memory tasks; Rosati et al. 2014), and contrast most highly with the folivorous Coquerel's sifaka. Although this difference was not significant, ruffed lemurs and Coquerel's sifakas scored highest and lowest, respectively, on this task. Similarly, sifakas were one of two species that did not significantly avoid the competitive experimenter in the reputation phase, in contrast to ruffed lemurs and ring-tailed lemurs, which did.

Additionally, other factors, such as dominance relationships, might influence social inhibitory control skills of our subjects. In all five species in our sample, females are dominant to males and have priority in food contests; thus, it may be particularly important for male lemurs to exercise inhibitory control when food is present. Though the difference was not significant, male lemurs tended to outperform females in the social inhibition task.

Lastly, it is interesting to note that at the individual level, performance on this task was not correlated with a measure of inhibitory control when solving a physical problem (MacLean et al. 2013). This finding suggests that the ability to assert inhibitory control may be affected by the context in which these skills are employed (Tsukayama et al. 2012; Bray et al. 2014a, b). However, at the species level, scores in the two tasks were positively but not significantly correlated. Because this analysis included only five species-level data points, we had limited statistical power to test this hypothesis. Nonetheless, given the apparent trend in this analysis (Fig. 4), it will be important to assess the correlation between these skills in larger phylogenetic studies (MacLean et al. 2014).

The experiment reported here presents a simple approach that can be used to evaluate social inhibition and is proof of concept that this task can be used with diverse species. Extending this approach to larger comparative samples will provide powerful opportunities to identify the social and ecological correlates of species differences in these skills.

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