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Analog number representations in mongoose lemurs (*Eulemur mongoz*): evidence from a search task

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Abstract A wealth of data demonstrating that monkeys and apes represent number have been interpreted as suggesting that sensitivity to number emerged early in primate evolution, if not before. Here we examine the numerical capacities of the mongoose lemur (*Eulemur mongoz*), a member of the prosimian suborder of primates that split from the common ancestor of monkeys, apes and humans approximately 47–54 million years ago. Subjects observed as an experimenter sequentially placed grapes into an opaque bucket. On half of the trials the experimenter placed a subset of the grapes into a false bottom such that they were inaccessible to the lemur. The critical question was whether lemurs would spend more time searching the bucket when food should have remained in the bucket, compared to when they had retrieved all of the food. We found that the amount of time lemurs spent searching was indicative of whether grapes should have remained in the bucket, and furthermore that lemur search time reliably differentiated numerosities that differed by a 1:2 ratio, but not those that differed by a 2:3 or 3:4 ratio. Finally, two control conditions determined that lemurs represented the number of food items, and neither the odor of the grapes, nor the amount of grape (e.g., area) in the bucket. These results suggest that mongoose lemurs have numerical representations that are modulated by Weber's Law.

Keywords Prosimians · Lemurs · Numerosity · Analog magnitude · Manual search

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Introduction

To understand the evolutionary precursors of human numerical ability, researchers have investigated the capacities of a handful of non-human primates, largely focusing on monkeys and apes. Prosimian primates (lemurs, lorises and galagos) diverged from other primates approximately 47–54 million years ago and are therefore a good model of ancestral primates, both phenotypically and cognitively (Yoder 2003). To date, there has been almost no research on the cognitive abilities of prosimians, and no studies have addressed their numerical ability (but see Santos et al. 2005). Here we test the numerical ability of mongoose lemurs (*Eulemur mongoz*).

A handful of primate species have been shown to possess numerical representations that are exquisitely modulated by Weber's Law, such that as numerical magnitude increases, a larger disparity is needed to obtain the same level of discrimination. For example, Brannon and Terrace (1998, 2000) found that accuracy in a numerical ordering task increased as the numerical disparity increased between the two numerosities compared (see also Smith et al. 2003). Similarly, Nieder et al. (2002) and Nieder and Miller (2003, 2004a, b) showed that behavioral accuracy and neuronal firing rate was modulated by the disparity between two numerosities in a same–different task. In both of these paradigms stimuli were visual arrays that carefully controlled for non-numerical cues. Other studies have shown that food choice in many primate species is modulated by Weber's Law. For example, the probability that a chimpanzee (*Pan troglodytes*) will choose the larger of two sets of discrete food items, increases as the numerical disparity of the quantities increases (e.g., Beran 2001). Similarly, Hauser et al. (2003) used a familiarization–discrimination paradigm and found that cotton-top tamarins (*Saguinus oedipus*) familiarized with a given number of syllables looked reliably longer at a speaker that emitted a novel number of syllables if the two quantities differed by a 1:2 or 2:3 ratio but not a 4:5 ratio.

In contrast, Hauser et al. (2000) tested rhesus monkeys (*Macaca mulatta*) in a task that allowed no learning, and found that rhesus monkeys appeared to have an upper limit on the number of food items they could represent. In their task, an experimenter sequentially baited each of two buckets with apple slices as a monkey watched, and the monkey was then allowed to approach either bucket. Each monkey was tested on a single trial. The dependent measure was the number of animals that chose the larger of the two quantities for each numerical contrast. Monkeys reliably chose the larger quantity with contrasts of 1 versus 2, 2 versus 3, and 3 versus 4, but were at chance on comparisons of 4 versus 5, 4 versus 6, 4 versus 8, and 3 versus 8. Thus, success appeared to be dependent on the size of the sets, and not on the ratio between the sets. This pattern of results differs markedly from the research on animal numerical ability reviewed above, which suggests that animals rely on a system for representing number that is rooted in analog magnitudes and obeys Weber's Law.

The results described above parallel findings with human infants that have also found performance to be limited by set size rather than Weber's Law. In a similar experimental design, Feigenson et al. (2002) found that 10- and 12-month-old infants reliably chose the larger quantity in comparisons of 1 versus 2, and 2 versus 3, but did not do so with comparisons that involved sets with four or more items (e.g., 2 vs 4, 3 vs 4, or 3 vs 6). That infants and monkeys succeeded with small number contrasts at a 1:2 or 2:3 ratio, but failed with larger number contrasts at the same ratio, suggests that the mechanism infants used to compare the two sets was limited by set size, and not subject to Weber's Law.

Using a second method, Feigenson and Carey (2003) tested whether human infants' search behavior was indicative of the number of objects remaining in an opaque box. Infants observed a number of balls being simultaneously placed into a box and were then allowed to retrieve all of the balls, or a subset of the balls. For example, to determine whether the infants' search behavior indicated that they represented two objects in a box, infants' search time was measured after they saw one ball go into the box and retrieved one ball, compared with search behavior after they saw two balls go in the box and retrieved one ball. A critical ingredient of this procedure is that a subset of the larger number of balls was surreptitiously removed so that the proprioceptive cues were identical in the comparison conditions. Infants searched significantly longer after retrieving one object from the box when they had originally seen two objects placed in the box, than when they had seen only one object placed in the box. Similarly infants searched longer after retrieving two objects when they had observed three objects placed in the box, compared with when they had observed two objects placed in the box. However, infants' search behavior did not provide any indication that they differentiated sets larger than three. Particularly interesting was that infants apparently completely failed to represent four objects. Infants who viewed four balls placed into a box (with two balls surreptitiously placed in a hidden compartment), and then retrieved two balls did not search longer than infants who had retrieved two balls after observing two balls placed in the box. This result was particularly surprising given that infants could have represented four as three or "three plus" but apparently did not (see also Feigenson and Carey 2005).

The set size limitations described above have been interpreted as evidence that human infants and rhesus monkeys rely on object-file representations in these contexts. The object-file model posits that a mental file or folder is opened for each element in a visual array (Hauser and Carey 1998; Leslie et al. 1998; Simon 1997; Uller et al. 1999). In this model there is no symbol that represents the numerosity of a set; instead, each element is represented by a file stripped of object features, such as color, shape, and size (see also Trick and Pylyshyn's1993, 1994 model, application of the FINST). A set size limitation arises because the visual system contains a limited number of object files that can be assigned to a given object, and a set can only be represented if there are a sufficient number of object files available (Pylyshyn and Storm 1988). Thus, if an organism's only means of representing number was through object-files, they could only represent sets of up to three or four objects.

Despite these interesting failures with large numerosities in the food choice task and the object search task, other studies demonstrate that human infants, like non-human animals, do possess a system for representing large numerical values (e.g., Brannon 2002; Brannon et al. 2004; Lipton and Spelke 2003; Xu 2003; Xu and Spelke 2000). Thus, an important question remains as to why the numerical system capable of representing large numerosities is not invoked in certain tasks such as the box search problem (e.g., Feigenson and Carey 2003) even when a monkey or infant is confronted with a problem that involves large values.

Here we use a task modeled after the box task used by Feigenson and Carey (2003) with mongoose lemurs (see also Santos et al. 2002). A lemur observed an experimenter place grapes successively into a single opaque bucket. The lemur was then allowed to retrieve all, or a subset, of the grapes. To prevent the lemurs from accessing all of the grapes placed in the bucket, some grapes were placed in a hidden compartment. Subsequently, search time was measured. If the lemurs represented the number of grapes they saw placed into the bucket, they should have continued to search for the remaining hidden grapes.

Methods

All experiments were conducted at the Duke University Primate Center, Durham, N.C., between April 2004 and August 2004. A total of nine mongoose lemurs participated in the study, four of whom were female. All subjects were adults (6–20 years old, mean = 13 years). Six or seven individuals participated in each condition. Six of the nine subject animals were pair housed and three were singly housed. Cage sizes ranged from 6 to 23 m^2. Only pair-housed animals living in a cage that allowed separation from the cage mate were selected for the experiment. During the course of our study, some pairs were moved to social groups or to cages that did not allow easy separation, and other animals were added to other research protocols; this made it impossible to test all nine animals in every condition. Animals were tested in the morning before their daily feeding.

Design

Subjects viewed grapes being placed into a green plastic bucket (23 cm in height with a diameter of 24 cm at the top and 16 cm at the bottom) filled with shredded paper, on the floor of their home enclosure, and were then allowed to retrieve some or all of the grapes they had observed being placed into the bucket. Trials were paired such that on one trial the lemur was allowed to retrieve all of the grapes it observed being successively placed into the container, and on a second trial (order counterbalanced) only a subset of the grapes were available for retrieval while the remaining grapes were surreptitiously placed into a false bottom (a hole with a 3-cm diameter covered by a Post-It note) and were therefore inaccessible to the subject. Subjects should have searched longer when they had not been allowed to retrieve all of the grapes that were placed into the bucket. There were five experimental conditions each consisting of two trials: 1-1 versus 2-1, 2-2 versus 4-2, 4-4 versus 8-4, 2-2 versus 3-2, 3-3 versus 4-3, where the first number in each trial referred to the number of grapes the experimenter placed into the bucket, and the second number referred to the number of grapes the subject was allowed to retrieve before search time was measured. In addition, two control conditions were conducted; an odor control and an area control. The odor control condition tested whether lemurs were motivated by odor cues rather than the number of grapes they saw placed in the bucket. This was a strong possibility because anthropoid primates are characterized by visual dominance over olfactory capacity, whereas lemurs and other prosimians have retained a more highly developed sense of olfaction, and engage in behaviors such as scent-marking (Irwin et al. 2004). Lemurs were given two 1-1 trials (retrieve and eat one grape after observing one grape placed in bucket). On one of these trials however, six grapes were secretly hidden in the false bottom prior to the start of the trial. If lemurs relied on odor cues, their search time should have been much greater on the trial in which six grapes remained in the false bottom.

In the area control condition, lemurs watched as two half-grapes were placed into the bucket and then allowed to retrieve a whole grape (0.5+0.5–1). This was accomplished by placing each of the half grapes into the false bottom of the bucket and simultaneously transferring a whole grape from the false bottom into the bucket. If the lemurs tracked the amount of grape, they should have been satisfied with having obtained a whole grape and should not have searched longer than in the comparison trial where they observed a single whole grape placed in the bucket and obtained one whole grape (e.g., 1-1). The order of the five experimental conditions was counterbalanced across subjects and only one condition was administered on any given day. The two control conditions were conducted after the experimental conditions.

Procedure

Lemurs were familiarized with the materials the day before their first test trial. In familiarization, the lemurs were shown an empty bucket and allowed to explore the bucket. The experimenter then successively placed two grapes into the bucket and allowed the lemur to retrieve both grapes. In test trials, the experimenter placed n grapes on the back of a clipboard placed on top of the bucket, in view of the subject. After the experimenter was certain the subject had looked at the collection of grapes, she began successively placing the grapes into the bucket. The experimenter ostentatiously waved her hand with the grape in front of the lemur, and then reached into the shredded paper, where she either released the grape into the mass of paper, or tucked it into the hidden compartment. The experimenter then immediately and quietly stepped away from the lemur and the bucket. Once the lemur had eaten the grapes that were accessible (chewing was visually pronounced and loud) the experimenter started a stop-watch, which emitted a faint beep, and turned her back toward the lemur. When 30 s had elapsed, the trial was terminated. On trials where lemurs did not find all of the grapes, or in trials when grapes were hidden in the false bottom, the experimenter removed them ostentatiously from the bucket, placing them simultaneously back into the grape container in full view of the lemur. It is important to note that the number of grapes retrieved and eaten was identical in each of the two paired test trials.

All trials were videotaped and coded by one or two observers who were blind to the experimental condition. One research assistant cued the tape to just after the lemur had finished eating the last retrieved grape and the beep of the experimenter's stopwatch had sounded. A second research assistant then coded search time during a 30-s window. A lemur was considered to be searching if its nose and/or hands were inside the bucket. Eighty percent of the trials were coded by a second observer, and reliability between the two observers was 99%.

Results

Figure 1a shows the average difference in search time between the paired trials in each experimental condition. For example, the 1 versus 2 difference score reflects the time spent searching on a 2-1 trial, minus the time spent searching on a 1-2 trial. Positive values indicate that the lemurs searched longer when they had yet to retrieve all of the grapes compared to when they had successfully retrieved all the grapes. As shown in Fig. 1a, difference scores were positive for all conditions with quantities that differed by a 1:2 ratio.

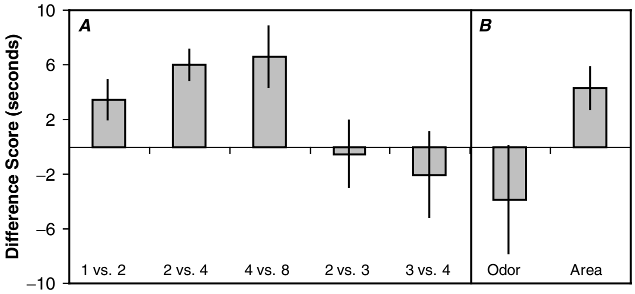

Fig. 1 **a** The average difference score for each experimental condition. Difference scores reflect the time lemurs spent searching on the trial in which they had not been allowed to retrieve all the grapes minus the time lemurs spent searching on the trial in which they had retrieved all the grapes. *Error bars* reflect standard error of the mean. **b** The average difference score for the two control conditions. *Error bars* reflect standard error of the mean

A 2×3 ANOVA examining the within-subject effect of trial type (grapes remaining vs all grapes retrieved) and the between-subject effect of the ratio of the number of grapes placed into the bucket to the number of grapes retrieved from the bucket (0.5, 0.67, or 0.75) on the time lemurs spent searching, revealed no main effects and an interaction between trial type and ratio ($F_{(2,29)}$=5.84, P=0.007). It is important to note that Bartlett's test of homogeneity of variance revealed that the variance in search time for the three ratios was not heterogeneous for the search time for the no grapes remaining trial type ($X^2_{(2)}$=2.3, P=0.316) nor for the grapes remaining trial type ($X^2_{(2)}$=0.73, P=0.696). To investigate the interaction between trial type and ratio, additional analyses were conducted on each ratio.

Lemurs searched significantly longer when grapes should have remained in the bucket than when all grapes had been retrieved on the 19 trials in which quantities differed by a 1:2 ratio as measured by both a non-parametric and a parametric test (Wilcoxon matched pairs test: n=19, z=3.54, P=0.0004; $t_{(18)}$=5.48, P=0.00003). Five out of the six lemurs tested in condition 1 (1-1 vs 2-1), all six lemurs tested in condition 2 (2-2 vs 4-2), and six out of the seven lemurs tested in condition 3 (4-4 vs 8-4) showed the predicted pattern (17/19, P=0.0003 binomial test).

By contrast, when the quantities differed by a 2:3 ratio (condition 4 = 2-2 vs 3-2) lemurs did not search longer when they had retrieved only a subset of the grapes that they had observed placed into the bucket by either a parametric or a non-parametric test (Wilcoxon matched pairs test: n=7, z=0.68, P=0.499; $t_{(6)}$=0.21, P=0.84) and five out of the seven lemurs tested showed the predicted pattern. Similarly, when the quantities differed by a 3:4 ratio (condition 5 = 3-3 vs 4-3) lemurs did not search longer when they had retrieved only a subset of the grapes by a parametric or a non-parametric test (Wilcoxon matched pairs test: n=6, z=0.31, P=0.753; $t_{(5)}$=0.67, P=0.53) and only two out of the six lemurs tested showed the predicted pattern. Thus, the interaction in the ANOVA was due to the fact that the lemurs searched significantly longer when grapes should have remained in the bucket than when they had retrieved all the grapes but only when these quantities differed by a 1:2 ratio.

Figure 1b shows the average difference in search time between the test trial types in the two control conditions. When lemurs watched one grape placed into the bucket and were allowed to retrieve one grape, their subsequent search time was not greater when six additional grapes were in the hidden compartment of the bucket. Thus, there was no significant difference between trials in the odor control condition by a non-parametric or a parametric test (Wilcoxon matched pairs test: n=6, z=0.73, P=0.463; $t_{(5)}$=0.98, P=0.37). Finally, lemurs did search longer after seeing two half grapes placed into a bucket and then retrieving a whole grape compared to when they had witnessed one whole grape placed into a bucket and retrieved one whole grape by both a non-parametric and a parametric test (Wilcoxon matched pairs test: n=6, z=2.2, P=0.028; $t_{(5)}$=2.8, P=0.037) and all six lemurs tested showed this pattern.

Discussion

These data suggest three important conclusions. First, this study provides initial evidence that prosimian primates represent number. Although it has been repeatedly demonstrated that many species of monkeys and apes represent number, the learning and cognition of prosimians has been largely ignored, and until now the numerical abilities of prosimians were untested. Our findings are particularly timely in that Santos et al. (unpublished research DOI 10.1007/s10071-005-0252-4) recently found evidence that lemurs track objects placed behind an opaque screen. That experiment, modeled after Wynn's violation of expectancy paradigm with human infants (Wynn 1992), tested whether lemurs look longer when the number of objects revealed behind a screen differs from the number that should be there, given the events the animal witnessed. Specifically, when lemurs watched as two lemons were successively placed behind a screen, they looked longer when the screen was lowered to reveal one or three lemons compared with the expected two lemons. Although these experiments did not test whether lemurs used alternative cues such as the cumulative surface area of the lemons, they nevertheless suggest that lemurs have object permanence and that they have representations that function to detect changes in quantity.

A second conclusion suggested by these results is that number discrimination in mongoose lemurs is modulated by Weber's Law and not strictly limited by set size. Lemurs discriminated quantities that differed by a 1:2 ratio but not quantities that differed by a 2:3 or 3:4 ratio. If lemurs were using an object-file system they should have been unable to represent eight and perhaps even four grapes in a bucket and yet six out of the seven animals tested in this condition searched longer when grapes should have remained in the bucket. These data therefore suggest that lemurs rely on analog magnitude representations of number rather than object-file representations. However, future studies should test mongoose lemurs and other species in this task, or comparable tasks, with additional large numerosities, and with better control over temporal cues to confirm this conclusion. In addition, it should be noted that our methods differ from those of Hauser et al. (2000) in that we tested individual animals in multiple counterbalanced conditions, whereas Hauser et al. conducted a single trial per animal and used between-subject experimental designs. It is possible that this difference in method encouraged our subjects to use analog magnitude representations rather than object-file representations. Future studies should explore the effect of repeated testing by comparing between- versus within-subject experimental designs in numerical tasks.

The third conclusion is that the precision with which mongoose lemurs make numerical discriminations may be inferior to that of New and Old World monkeys. In the familiarization–discrimination paradigm used by Hauser et al. (2003), tamarin monkeys successfully discriminated sequences of syllables that differed by a 1:2 and 2:3 ratio but not a 4:5 ratio. In contrast, the lemurs in our experiment failed to differentiate pairs with a 2:3 or 3:4 ratio. It remains to be determined whether additional training would allow mongoose lemurs to make more precise numerical discriminations such as those observed in rhesus macaques which have successfully discriminated numerosities that differ by a 4:5 ratio (e.g., Brannon and Terrace 2000). It will be important to test each species in multiple numerical assays before making firm conclusions about the numerical ratio required for successful discrimination.

Mongoose lemurs' search behavior in the present paradigm appears to be controlled by the number of grapes they observe being placed into the bucket. In contrast, in food choice tasks where an animal watches as two buckets are baited and is then allowed to choose one quantity (e.g., Hauser et al. 2000), animals should be motivated to choose the larger continuous amount of food rather than the larger number of food items. In our task two quantities were not pitted against each other and the amount of grape was apparently not salient in this context. Although it is possible that lemurs in our task could not see the grapes well enough to encode a continuous attribute of the grapes, this possibility does not detract from the fact that lemurs apparently encoded a numerical aspect of the test events. For example, the lemurs may have relied on the number of hand movements made by the experimenter rather than the number of grapes, however, this would still be a numerical representation (see Beran and Beran 2004). It is important to note however, that our experiment does not rule out the possibility that the lemurs encoded the cumulative duration of the experimenter hand movements rather than number per se. Future research should test these alternative hypotheses.

In conclusion, although prosimian primates diverged from the ancestors of monkeys and apes some 54 million years ago, these results suggest that the basic cognitive machinery necessary for detecting numerical aspects of the environment were present in their common ancestor. This may not be surprising since there are numerous studies showing sensitivity to number in non-primate species (e.g., Meck and Church 1983). A challenge of future studies in animal numerical cognition will be to map similarities and differences in numerical cognition between species to determine whether shared abilities are inherited from a common ancestor or reflect adaptations to solve similar social or ecological problems. Toward this end, researchers should quantify the precision with which primates and other animals make numerical discriminations and whether such variability can be explained by phylogenetic factors or socio-ecology.

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