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ORIGINAL ARTICLE

Laurie R. Santos · Jennifer L. Barnes · Neha Mahajan

Expectations about numerical events in four lemur species (*Eulemur fulvus*, *Eulemur mongoz*, *Lemur catta* and *Varecia rubra*)

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Abstract Although much is known about how some primates—in particular, monkeys and apes—represent and enumerate different numbers of objects, very little is known about the numerical abilities of prosimian primates. Here, we explore how four lemur species (*Eulemur fulvus*, *E. mongoz*, *Lemur catta*, and *Varecia rubra*) represent small numbers of objects. Specifically, we presented lemurs with three expectancy violation looking time experiments aimed at exploring their expectations about a simple 1+1 addition event. In these experiments, we presented subjects with displays in which two lemons were sequentially added behind an occluder and then measured subjects' duration of looking to expected and unexpected outcomes. In experiment 1, subjects looked reliably longer at an unexpected outcome of only one object than at an expected outcome of two objects. Similarly, subjects in experiment 2 looked reliably longer at an unexpected outcome of three objects than at an expected outcome of two objects. In experiment 3, subjects looked reliably longer at an unexpected outcome of one object twice the size of the original than at an expected outcome of two objects of the original size. These results suggest that some prosimian primates understand the outcome of simple arithmetic operations. These results are discussed in light of similar findings in human infants and other adult primates.

Keywords Prosimians · Lemurs · Expectancy violation paradigm · Number representation

Introduction

The question of how primates represent number has received a great deal of attention in the past few decades (e.g., Boysen and Capaldi 1993; Gallistel 1990; Hauser 2000). Researchers have learned, for example, that a number of different primate species can be trained to discriminate different quantities of objects (Beran et al. 1998; Beran and Rumbaugh 2001; Boysen et al. 1996; Brannon and Terrace 1998, 2000; Matsuzawa 1985). In addition, a few extensively trained primates have demonstrated even more sophisticated abilities, such as the capacity to add and subtract different numerosities (e.g., Beran 2004; Rumbaugh et al. 1987), to represent the ordinal relationships between numbers (e.g., Biro and Matsuzawa 2001; Brannon and Terrace 1998, 2000), and to map symbols onto different numerical quantities (e.g., Biro and Matsuzawa 2001; Boysen and Berntson 1989; Matsuzawa 1985; Rumbaugh and Washburn 1993; Washburn and Rumbaugh 1991).

Unfortunately, although the above studies elegantly demonstrate what primates can learn about number after extensive training, it is often difficult to discern what these data tell us about how primates naturally represent number in the absence of training. To deal with this issue, some investigators have begun developing new experimental methodologies to assess how primates spontaneously reason about number. One such methodology is the looking time paradigm, a methodology originally developed for use with human infants. The logic behind the looking time method is that subjects will look longer at events that they see as violations of the physical or social world (e.g., Hauser and Carey 1998). As such, researchers can present subjects with expected and unexpected events and examine differences in subjects' duration of looking as a measure of what they expect about the different events.

Over the past decade, researchers have successfully used looking techniques to explore numerical representations in two primate species—rhesus monkeys (*Macaca mulatta*) and cotton-top tamarins (*Saguinus oedipus*). Using such looking assays, we have learned that these two species spontaneously add and subtract small numbers of objects

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This revised version was published online in March 2005 with corrections to Fig. 6.

L. R. Santos (✉) · J. L. Barnes · N. Mahajan
Department of Psychology, Yale University,
New Haven, CT 06520, USA
e-mail: laurie.santos@yale.edu
Tel.: +1-203-432-4524
Fax: +1-203-432-7172

(Hauser and Carey 2003; Hauser et al. 1996; Uller et al. 2001), can discriminate small numbers of sounds (Hauser et al. 2002), and can represent the approximate number of large quantities of objects and sounds (Flombaum et al. in press; Hauser et al. 2002). Taken together, these looking studies provide evidence that some non-human primates not only make expectations about number, but do so spontaneously and in the absence of explicit training.

The evidence that primates spontaneously represent numerical information fits with an emerging view—often referred to as the core knowledge hypothesis—that many of the building blocks of human representational systems may be phylogenetically ancient and, as such, present in other primate species (Hauser and Carey 1998; Hauser and Spelke 2005; Spelke 2000). This core knowledge view argues that humans and other animals begin life with a suite of conceptual building blocks in place and use these representations to guide their learning throughout life. In support of this view, developmental psychologists have amassed a wealth of evidence that human infants also represent some aspects of number spontaneously and from a very early age. Before their first birthday, human infants can spontaneously discriminate small numbers of objects and events (Feigenson et al. 2002; Wynn 1992), enumerate collections of objects (Chiang and Wynn 2000; Wynn et al. 2002), add and subtract small numbers of occluded objects (Koechlin et al. 1997; Simon et al. 1995; Wynn 1992), and represent the approximate numerosity for larger quantities of objects and sounds (Lipton and Spelke 2003; Xu 2003; Xu and Spelke 2000). In short, when tested with nearly identical empirical methods, human infants seem to reason about numerical information in much the same way as cotton-top tamarins and rhesus monkeys.

Because of its unparalleled ability to compare across different species, the looking time procedure has become a powerful empirical tool for exploring how animals spontaneously represent number (as well as other domains of knowledge, see Hauser 2000 for review). Because this technique relies simply on a subject's duration of looking, it is able to circumvent many of the performance problems that often plague comparative research. Unfortunately, however, this technique has thus far been restricted to only a handful of primate species (see West and Young 2002 for an exception with a species from a different taxa—domestic dogs, *Canis familiaris*). This is unfortunate, as comparisons across different primate species are needed to determine when different cognitive capacities evolved (i.e., whether a particular capacity was present in an evolutionarily ancient common ancestor or whether it evolved more recently in primate evolution). Moreover, observing cognitive similarities and differences among related primate species can help to illuminate both the neural mechanisms underlying a particular capacity (e.g., species differences in a capacity can result from species differences in certain brain structures), as well as the evolutionary selection pressures that led to the development of that capacity (e.g., species differences in a capacity can result from species differences in ecology, social structure, etc.).

Here, we extend looking time measures of number to a group of primates that have rarely before been tested in cognitive tasks—the prosimians. In particular, we explore whether four lemur species—ring-tailed lemurs, mongoose lemurs, red-ruffed lemurs, and brown lemurs—spontaneously make expectations about the number of objects hidden behind a screen. Lemurs, like the other prosimian primates, have largely been neglected in studies of cognition. Although some work has explored how lemurs perform in discrimination learning tasks (see Tomasello and Call 1997 for an elegant review of this work), very little is known about their cognitive abilities more generally and their numerical understanding in particular. Lewis et al. (2005) have found some evidence that at least one lemur species (the mongoose lemur) can discriminate between different quantities of hidden objects in a searching task. Here, we use looking time to examine another aspect of numerical understanding—the ability to add and subtract small numbers of items—in four lemur species.

We chose to begin our investigation with one of the most widely used looking time tests of numerical knowledge: a simple 1+1 addition event (e.g., Feigenson et al. 2002; Hauser and Carey 2003; Hauser et al. 1996; Koechlin et al. 1997; Simon et al. 1995; Uller et al. 2001; Wynn 1992). In this event, subjects watch as two objects are sequentially added behind an occluder. The occluder is then removed to reveal either a possible outcome of two objects or an impossible outcome of only one object. We predict that subjects will look longer at unexpected outcomes of one object if and only if they are able to enumerate the correct number of objects involved in this event.

Experiment 1: 1+1=2 versus 1

Methods

Subjects

We tested 21 lemurs living at the Lemur Conservation Foundation's Myakka City Reserve in Myakka City, Florida: 6 ring-tailed lemurs *Lemur catta* (4 adult males and 2 adult females), 6 brown lemurs *Eulemur fulvus* (3 adult males and 3 adult females), 5 mongoose lemurs *Eulemur mongoz* (2 adult males, 2 adult females and 1 juvenile female), and 4 red-ruffed lemurs *Varecia rubra* (2 adult males and 2 adult females). All individuals were born in captivity and relocated to the reserve within the past 5 years, with the exception of the juvenile mongoose lemur who was born at the reserve. The Myakka City Lemur Reserve consists of a 13-acre forest enclosure surrounded by an electrified chain link fence. Animals at the reserve are free to range throughout the enclosure. The existing indigenous vegetation in the forest has been supplemented by plantings of mango, passion fruit, guava, grapes, banana, persimmon, and bamboo species already found to be widespread in Florida.

Although animals spend the majority of their time ranging freely, the reserve also has a number of outdoor and indoor enclosures that can be used to isolate animals during times of environmental stress or poor health. The animals at the reserve are habituated to humans, as caretakers and experimenters work daily on the reserve around the animals. The lemurs are fed a diet of lemur chow and fruit, but also consume foods occurring throughout the forests. Water is available at a number of locations throughout the enclosure.

Although we tested all 21 lemurs in experiment 1, we obtained usable data from only 18 lemurs (6 ring-tailed lemurs, 6 mongoose lemurs, 4 brown lemurs, and 2 red-ruffed lemurs); other subjects' data could not be used due to interference from other animals, disinterest during presentation or isolation, or experimenter error. Subjects were tested over the course of 16 days; individuals were tested in a randomized order such that individuals from multiple species were tested on individual testing days.

Apparatus

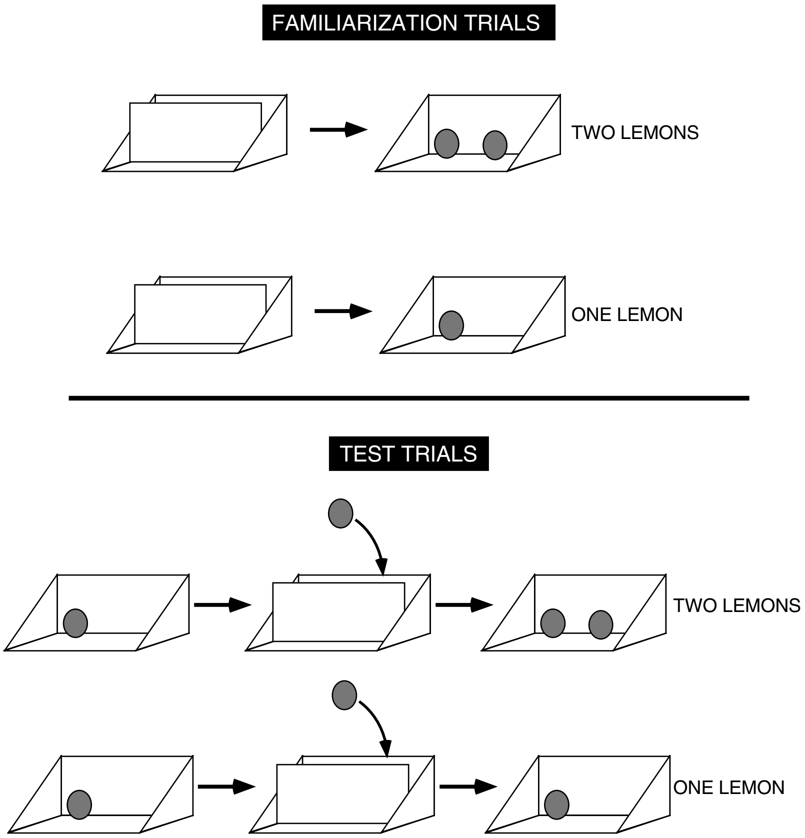
We presented subjects with events in which an experimenter placed two lemons onto a stage behind an occluder. The testing apparatus consisted of a black foamcore stage (51 cm × 18 cm × 18 cm) and an occluder (46 cm × 33 cm × 10 cm) that could sit on the stage, blocking it from the subject's view. We affixed a shelf to the back of the occluder such that an experimenter could place an object behind the occluder and onto the shelf while appearing to place the object onto the stage. We used two equally sized lemons as stimuli.

Procedure

Lemurs were tested inside one of their familiar outdoor enclosures (1.00 m × 3.92 m × 2.23 m). Before testing, an experimenter lured subjects into one of these enclosures using a small food treat (e.g., a grape or raisin); subjects typically entered quickly and voluntarily. Once a subject was isolated inside the enclosure, the experimenters presented the familiarization and test events from an adjacent enclosure. Two experimenters who were familiar to the subjects ran each session. The first served as the presenter, operating the stage and display objects. The other served as the cameraperson, filming the session from just behind the presenter.

Each session consisted of four trials: two familiarization trials and two test trials (see Fig. 1). As in looking time studies previously run with other primates (e.g., Hauser et al. 1996), familiarization and test trials were run one after the other such that test trials followed immediately after the completion of the two familiarization trials. Subjects were treated with a raisin in between each trial in order to maintain their continued interest in the display. Familiarization trials began with the occluder sitting on the stage. The presenter began by getting the subject's attention and next lifted the occluder to reveal one of two outcomes: a "one lemon" outcome, in which one lemon was revealed on the stage, or a "two lemons" outcome, in which two lemons were revealed on the stage. After the outcome was revealed, the presenter called "start" and the subject's

Fig. 1 A depiction of the familiarization and test trials used in experiment 1



looking was recorded for the next 10 s. During this 10-s period, the presenter turned her head away so as to avoid looking at either the subject or the stage. The order of these two familiarization trials was counterbalanced across subjects.

After familiarization, subjects received two test trials. Both test trials began with an empty stage. Next, the presenter placed a lemon visibly on the stage, and then placed the occluder on the stage such that it blocked the lemon from the subject's view. The experimenter presented a second lemon and placed it behind the occluder. Finally, the occluder was lifted to reveal one of two test outcomes: a "two lemons" outcome, in which both of the lemons placed behind the occluder were revealed on the stage, or a "one lemon" outcome, in which only one lemon was revealed on the stage (the other had been surreptitiously placed on the shelf on the back of the occluder and removed without the subject's knowledge). If subjects were tracking the number of objects placed onto the stage, than the one lemon outcome should be considered unexpected. After the outcome was revealed, the presenter called "start" and the subject's looking was recorded for the next 10 s. During this 10-s period, the presenter turned her head away so as to avoid looking at either the subject or the stage. The order of these two test trials was counterbalanced across subjects.

Coding

Videotapes were acquired digitally onto an iBook computer using iMovie software and were later analyzed frame-by-frame in Adobe Premiere. A single experimenter who was blind to the experimental condition coded the duration of subjects' looking across all trials. A look for the purpose of this experiment was defined as any period of time in which the subject's head and eyes were oriented towards the display. After the initial coding, a second experimenter who was also blind to the experimental condition coded all test trials to establish reliability ($r=0.90$).

Results

We performed a repeated-measures ANOVA with trial-type (familiarization or test) and condition (one lemon or two lemons) as within-subject variables and species as a between-subject variable (see Fig. 2). There was no main effect of species ($F_{(3,14)}=0.51$, $P=0.68$) or trial-type ($F_{(1,14)}=0.01$, $P=0.97$). We did observe a main effect of condition ($F_{(1,14)}=4.97$, $P=0.04$). Collapsing across familiarization and test trials, subjects looked longer at one lemon events (mean±SE= 4.35±0.35 s) than two lemon events (3.79±0.31 s). We also found a significant interaction between condition and trial-type ($F_{(1,14)}=49.03$, $P<0.0001$). Although there was no difference in looking time across one lemon and two lemon familiarization trials (3.74±0.51 s vs 4.35±0.34 s, $t_{(17)}=1.55$, $P=0.14$), subjects did exhibit a significant difference in looking across the two test conditions ($t_{(17)}=6.90$, $P<0.0001$). Subjects looked reliably longer at the one lemon test event (4.95±0.46 s) than two lemons test event (3.22±0.49 s). This pattern was confirmed using non-parametric analyses (Wilcoxon signed rank: $Z=3.72$, $P<0.0002$). All individuals showed the predicted pattern, looking longer at the one lemon test outcome than at the two lemon test outcome. We next explored how different species performed on the test trials. Each species, on average, demonstrated the same overall pattern, longer looking at the one lemon test than the two lemon test: brown lemurs (5.15±1.25 vs 4.20±1.33 s, $n=6$), mongoose lemurs (5.12±0.92 vs 3.40±0.40 s, $n=4$), ring-tailed lemurs (4.44±0.34 vs 2.37±0.52 s, $n=6$) and red-ruffed lemurs (5.58±0.15 vs. 2.48±0.25 s, $n=2$). As such, we observed no interaction between condition, trial-type, and species ($F_{(3,14)}=2.30$, $P=0.12$); this suggests that all species showed the test trial effect equally.

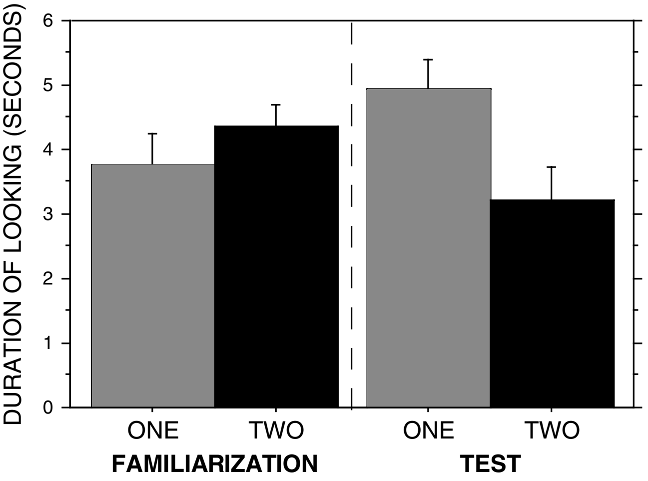


Fig. 2 Duration of looking in s (mean±SE) across familiarization and test conditions in experiment 1

Discussion

After witnessing an event in which two lemons are sequentially added behind a screen, lemurs look longer at an unexpected final outcome of one lemon than an expected final outcome of two lemons. This result was not due to a baseline preference for looking at less objects; subjects showed no preference for either one or two lemons on familiarization trials. Interestingly, we observed no significant differences across the different lemur species; all four species demonstrated a reliable looking preference for the unexpected outcome of one lemon.

These results are important for two reasons. First, they show that the looking time method can successfully be used with a distantly related primate group—the lemurs. This is the first demonstration of interpretable looking time data from a prosimian primate, and therefore paves the way for future looking time studies with these and other prosimian species. Second, our results provide some of the first evidence to date that lemurs spontaneously enumerate objects hidden behind a screen (see Lewis et al. 2005 for similar successes in mongoose lemurs). Like cotton-top tamarins and rhesus macaques, lemurs seem to not only possess some expectations about the behavior of occluded objects, but are also able to quantify them across simple operations.

One problem with the above study, however, is that it is unclear exactly why subjects looked longer at the unexpected event. One possibility is that our lemur subjects had an exact expectation about the outcome of the 1+1 event. In other words, they understood that the outcome of the 1+1 event should involve exactly two objects. Alternatively, subjects may have discriminated between the expected and unexpected outcomes simply because they expected to find more than one object. As such, subjects could show successful discrimination on this task even without recognizing exactly how many objects should be behind the occluder.

We distinguish between these alternatives in experiment 2. Specifically, we present subjects with the same 1+1 event but with different final outcomes: a possible outcome of two objects and an impossible outcome of three objects. If subjects succeeded in experiment 1 merely by detecting that more objects should be present, then subjects should fail to discriminate between expected and unexpected test trials in experiment 2, looking equally at outcomes of two and three objects. However, if subjects expect the event to end with exactly two objects behind the screen, then they should successfully discriminate between the two test outcomes, demonstrating longer looking to the incorrect three object outcome.

Experiment 2: 1+1=2 versus 3

Methods

Subjects

We tested the same 21 lemurs in experiment 2. Testing occurred approximately 1 month after the completion of experiment 1. We obtained usable data from 17 of these animals (5 ring-tailed lemurs, 6 brown lemurs, 3 mongoose lemurs, and 3 red-ruffed lemurs); other subjects' data could not used due to interference from other animals, disinterest during presentation or isolation, or experimenter error.

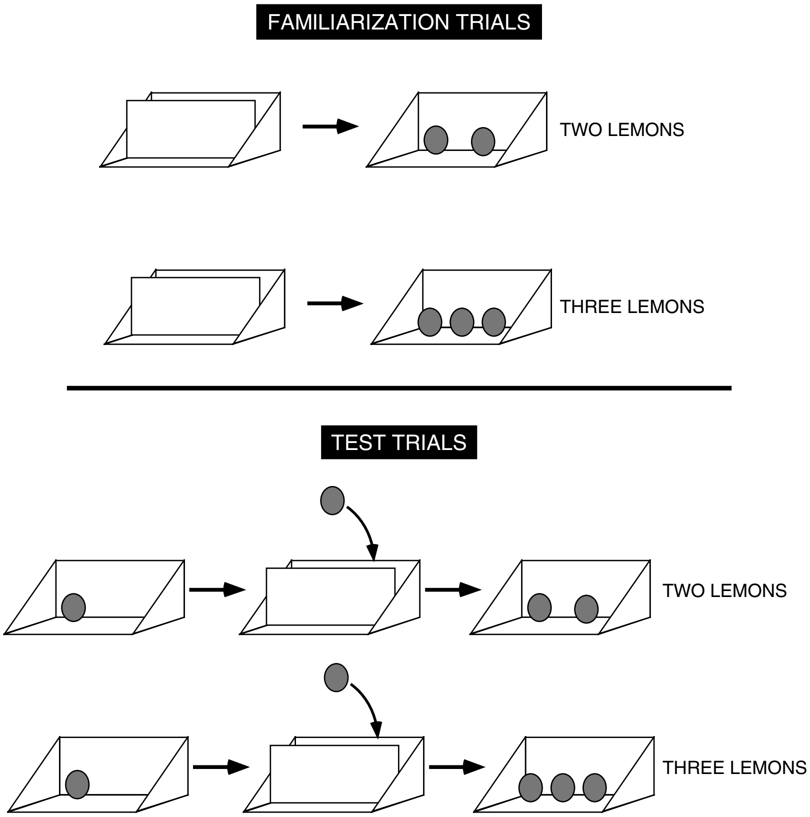
Apparatus

We used the same stage as in experiment 1, but this time used three equally sized lemons as stimuli.

Procedure

The procedure was similar to that of experiment 1 except for the changes noted below (see Fig. 3). Sessions again consisted of two familiarization trials and two test trials. Familiarization trials began with the occluder sitting on the stage. The presenter then lifted the occluder to reveal one of two outcomes: a "two lemons" outcome, where two lemons

Fig. 3 A depiction of the familiarization and test trials used in experiment 2



were revealed on the stage (as in experiment 1); or a "three lemons" outcome, in which three lemons were revealed on the stage. The order of these two familiarization trials was counterbalanced across subjects.

After familiarization, subjects again received two tests trials. Both test trials began with an empty stage. The presenter placed one lemon visibly on the stage, placed the occluder down such that it blocked this lemon from the subject's view, presented a second lemon and placed this lemon behind the occluder. The occluder was then lifted to reveal one of two test outcomes: a "two lemons" outcome, in which both of the lemons placed behind the occluder were revealed on the stage, or a "three lemons" outcome, in which three lemons were revealed on the stage (the extra third lemon had been surreptitiously placed on the occluder's shelf and placed onto the stage without the subject's knowledge). If subjects were tracking the exact number of objects placed onto the stage, then the three lemons outcome should be considered unexpected. The order of these two test trials was again counterbalanced across subjects.

Results

We performed a repeated-measures ANOVA with trial-type (familiarization or test) and condition (two lemons or three lemons) as within-subject variables and species as a between-subject variable (see Fig. 4). All main effects were not significant (species: $F_{(3,13)}=2.14$, $P=0.14$; trial-type: $F_{(1,13)}=0.94$, $P=0.35$; condition: $F_{(1,13)}=0.10$, $P=0.76$). We did, however, find a significant interaction between condition and trial-type $F_{(1,13)}=4.53$, $P=0.05$). Although there was no difference in looking time across two and three lemon familiarization trials (mean±SE: 3.52±0.50 s vs 3.17±0.46 s, $t_{(16)}=0.65$, $P=0.53$), subjects did exhibit a significant difference in looking across the two test conditions $t_{(16)}=2.81$, $P=0.01$). Subjects looked reliably longer at the three lemons test event (3.38±0.36 s) than the two lemons test event (2.38±0.32 s). Non-parametric Wilcoxon signed rank analyses confirmed this pattern of results $Z=2.60$, $P=0.009$). Only 3 of the 17 individuals did not show the predicted pattern of looking longer at the three lemon test outcome than at the two lemon test outcome. We then explored how different species performed on the test trials. All species showed a mean effect of looking longer at the three lemon test than the two lemon test: brown lemurs (3.53±0.69 vs 1.86±0.44 s, $n=6$), mongoose lemurs (3.36±0.62 vs 3.34±0.61 s, $n=3$), ring-tailed lemurs (3.09±0.77 vs 1.83±0.62 s, $n=5$) and red-ruffed lemurs (3.59±1.01 vs 3.37±0.65 s, $n=3$). As such, we observed no interaction between condition, trial-type, and species $F_{(3,13)}=0.91$, $P=0.46$).

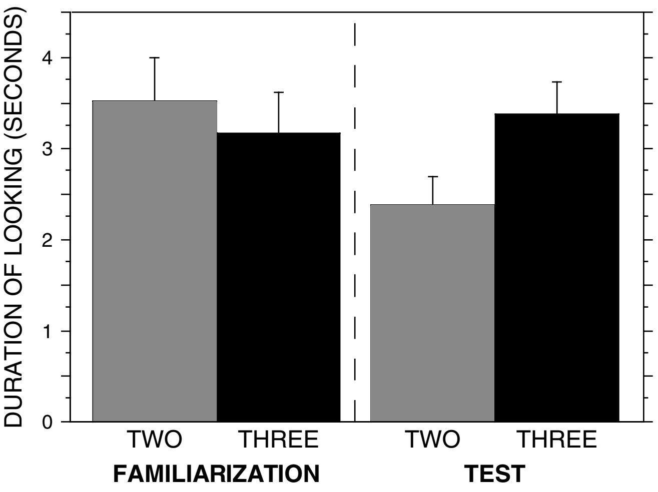


Fig. 4 Duration of looking in s (mean±SE) across familiarization and test conditions in experiment 2

Discussion

Experiment 2 was designed to clarify how our lemur subjects succeeded in discriminating correct and incorrect outcomes in experiment 1. After witnessing a 1+1 event in this second study, lemurs looked longer at an unexpected outcome of three objects than a consistent outcome of two objects. These data suggest that lemurs were not simply expecting that a 1+1 event should yield an outcome of "more than one object" or "more lemon." Instead, like cotton-top tamarins (Uller et al. 2001) and rhesus monkeys (Hauser and Carey 2003), lemurs seem to have rather precise expectations about the outcome that should result from this operation.

Although experiments 1 and 2 demonstrate that lemurs have relatively specific expectations about the outcome of a 1+1 event, the previous experiments do little to investigate the way in which subjects represent the outcome of this addition event. One possibility is that our subjects are computing a numerical outcome; in other words, our lemurs attend to the number of objects behind the screen and therefore look longer when an incorrect numerical outcome is revealed. Alternatively, our subjects could succeed in this task without the use of numerical information per se. It is possible that our subjects attended to another continuous property of the display that happens to be correlated with number (e.g., the amount of yellow-stuff on the stage, the area of objects on the stage) and looked longer at test outcomes in which the amount of this continuous variable was incorrect (see Clearfield and Mix 1999, 2001; Feigenson et al. 2002 for similar interpretations of results with human infants).

We used experiment 3 to control for at least one of these potential non-numerical confounds: the amount of lemon stuff present on the stage. As identified by other researchers (e.g., Hauser and Carey 2003), it is possible that subjects represent a 1+1 event simply in terms of the amount of substance present on the stage; an impossible outcome of 1 object is therefore seen as unexpected not because of a numerical violation, but simply because some expected lemon "stuff" is missing from the stage. To test this alternative explanation, experiment 3 controlled for the amount of total lemon stuff present in both the expected and unexpected test outcomes. Specifically, we presented subjects with two new test outcomes, both of which presented the same amount of lemon stuff on the stage (i.e., the same amount of total lemon weight): an expected outcome of two lemons and an unexpected outcome of one big lemon (equal in weight to the two small lemons). If subjects succeeded in experiments 1 and 2 based on an expectation about the amount of total lemon stuff present, then they should fail to discriminate between the expected and unexpected outcomes in experiment 3. If, however, they expect the correct numerical outcome of exactly two smaller lemons, then they should successfully discriminate between the two test outcomes, demonstrating longer looking to the incorrect one large object outcome.

Experiment 3: 1 (small) + 1 (small) = 2 (small) versus 1 (big)

Subjects

We tested twenty lemurs, all of whom had been previously tested in experiments 1 and 2. Testing occurred approximately 4 months after the completion of experiment 2. Usable data was obtained for 16 of these subjects: 3 red-ruffed lemurs, 3 mongoose lemurs, 6 brown lemurs, and 4 ring-tailed lemurs. Data from the remaining 4 could not be used due to experimental error or subject inattention during presentation.

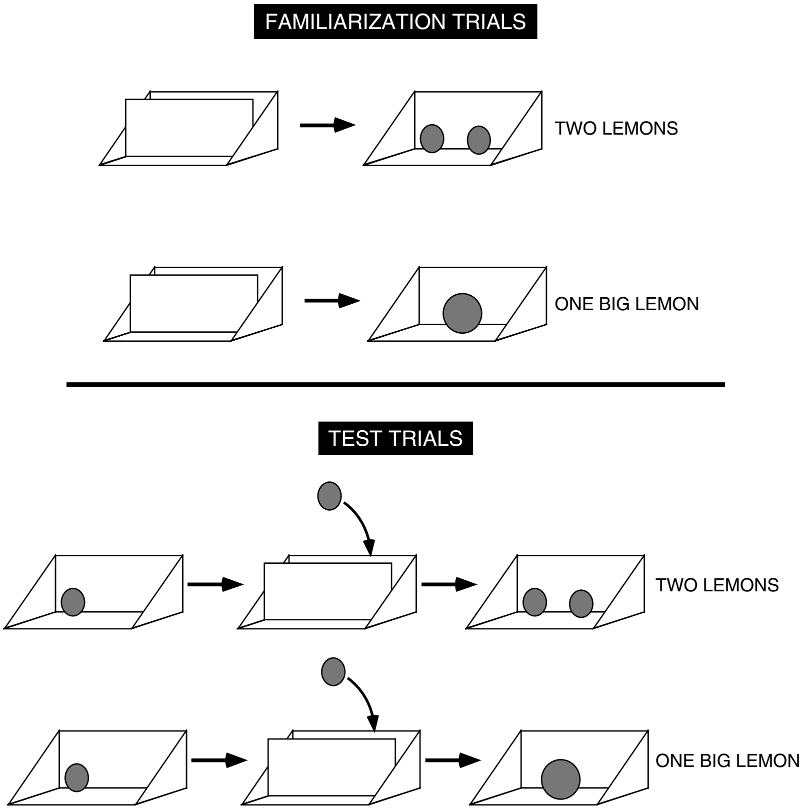
Apparatus

We used the same stage as in experiments 1 and 2. The stimuli used were three lemons: one big lemon (165 g) and two smaller lemons whose total combined weight was equal to that of the big lemon.

Procedure

We implemented a similar procedure to that used in experiments 1 and 2 with the following changes (see Fig. 5). Each testing session again began with two familiarization trials; in these familiarization trials, an occluder was lifted to reveal either the one big lemon or the two small lemons respectively. We then presented subjects with two test trials in a counterbalanced order. The test trials began with an empty stage. The presenter then placed one small lemon on the stage and lowered the occluder in front of this lemon, thus blocking it from the subject's view. A second small lemon was then placed behind the occluder on the stage. The presenter then lifted occluder to reveal one of two outcomes: a "two lemons" outcome (expected) or a "one big lemon" outcome (unexpected). If subjects in experiments 1 and 2 distinguished between expected and unexpected outcomes based on the amount of lemon stuff present on the stage (i.e., the combined weight of the lemons), then subjects should not distinguish between the expected and unexpected outcomes in this experiment. If, however, our

Fig. 5 A depiction of the familiarization and test trials used in experiment 3



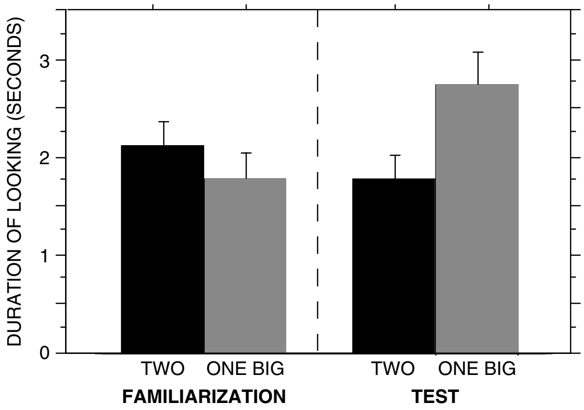


Fig. 6 Duration of looking in s (mean±SE) across familiarization and test conditions in experiment 3

subjects were attending to the number of objects behind the screen, then they should expect to see the correct numerical outcome of exactly two small lemons. In this case, we would expect them to look longer at the incorrect numerical outcome of one big lemon, despite the fact that the weight of the lemons was held constant across the two test conditions.

Results

We performed a repeated-measures ANOVA with trial-type (familiarization or test) and condition (two small lemons or one big lemon) as within-subject variables and species as a between-subject variable (see Fig. 6). All main effects were not significant (species: $F_{(3,12)}=0.49$, $P=0.70$; trial-type: $F_{(1,12)}=0.69$, $P=0.42$; condition: $F_{(1,12)}=2.16$., $P=0.17$). We did, however, find a significant interaction between condition and trial-type ($F_{(1,12)}=12.84$, $P=0.004$.). Although there was no difference in looking time across one big and two small lemons familiarization trials (mean±SE: 1.76±0.27 s vs 2.11±0.25 s, $t_{(15)}=1.21$, $P=0.24$), subjects did exhibit a significant difference in looking across the two test conditions ($t_{(15)}=3.56$, $P=0.003$). Subjects looked reliably longer at the one big lemon test event (2.74±0.36 s) than the two small lemons test event (1.77±0.24 s). Nonparametric Wilcoxon signed rank analyses confirmed this pattern of results ($Z=2.90$, $P=0.004$). All individuals but one showed the predicted pattern, looking longer at the one big lemon test outcome than at the two small lemons test outcome. We then explored how different species performed on the test trials. All species showed a mean effect of looking longer at the one big lemon test than the two small lemons test: brown lemurs (2.67±0.48 vs 1.82±0.41 s, $n=6$), mongoose lemurs (2.67±0.91 vs 2.37±0.57 s, $n=3$), ring-tailed lemurs (2.55±1.18 vs 1.43±0.60 s, $n=4$) and red-ruffed lemurs (3.18±0.55 vs 1.53± 0.19 s, $n=3$). As such, we observed no interaction between condition, trial-type, and species ($F_{(3,12)}=1.08$, $P=0.39$); this suggests that all species showed the test trial effect equally.

Discussion

Experiment 3 was designed to clarify how our lemur subjects succeeded in discriminating correct and incorrect numerical outcomes in experiments 1 and 2. After witnessing a 1+1 event in this third study, lemurs looked longer at a numerically inconsistent outcome of one larger object than at a numerically consistent outcome of two smaller objects. These data suggest that lemurs were not simply expecting that a 1+1 event should yield an outcome of "twice as much lemon stuff." Instead, even when the weight of the two outcomes is held constant, lemurs seem to have expectations about the outcome of this arithmetic operation. This suggests that, like rhesus monkeys (Hauser and Carey 2003) and tamarins (Uller et al. 2001), lemurs represent the outcome of a 1+1 event not in terms the amount of stuff present on the stage, but in terms of numerosity.

Experiment 3 demonstrates that our subjects cannot be using the weight of the lemons alone as a means of distinguishing between expected and unexpected outcomes. Nevertheless, it is possible that they are using some other continuous variable more subtly correlated with number to succeed on this task. Again, our present data are silent as to whether or not one of these other continuous variables might account for our subjects' performance in these experiments. Future experiments with these species could profit from teasing apart these variables and exploring even more precisely the representations lemurs are using in this task.

General discussion

Like human infants (e.g., Feigenson et al. 2002; Koechlin et al. 1997; Simon et al. 1995; Wynn 1992), rhesus macaques (Hauser et al. 1996), and cotton-top tamarins (Uller et al. 2001), adult lemurs are able to successfully form expectations about the exact outcome of a simple 1+1 addition event. Our subjects' performance indicates that lemurs have the ability to track objects hidden behind occluders as well as the capacity to enumerate these occluded objects across time and motion. In addition, our results suggest that lemurs are able to quantify small sets of objects spontaneously; as our looking tasks involve no training, our results necessarily tap into capacities that are naturally available to these animals without extensive preparation.

We see at least two important implications of the present results. First, our experiments are the first of their kind to extend the looking time methodology to prosimian primates. The results of experiments 1, 2, and 3 suggest that lemurs (and potentially other strepsirhine primates) can be tested using expectancy violation measures. This indicates that looking time methods can be used not just for future studies of the numerical capacities of lemurs, but also to explore cognition in prosimian primates more generally. For this reason, we hope that our experiments will provide the first step in a much larger investigation into the cognitive abilities of prosimian primates.

A second, more theoretical implication of our results concerns the evolutionary history of human core knowledge abilities. As discussed above, an assumption of the core knowledge hypothesis is that humans may share some core numerical abilities with other animals (Hauser and Carey 1998; Hauser and Spelke 2004). To date, however, researchers have only observed these purportedly shared abilities in a few monkey species and one non-primate (e.g., the domestic dog, West and Young 2002). Our lemur findings suggest that at least some of the numerical abilities observed in New and Old World monkey species extend to prosimian primates as well (see also Lewis et al. 2005). Specifically, our data suggest that both anthropoid and strepsirhine primates have the capacity to represent simple arithmetic operations. As such, our data provide some of the first available evidence that at least one aspect of human core knowledge—the ability to enumerate small numbers of occluded objects—might extend quite widely across the primate order. These data, combined with data from other mammalian taxa, raise the possibility that other aspects of core knowledge might be shared throughout the animal kingdom as well.

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References

Beran MJ (2004) Chimpanzees (*Pan troglodytes*) respond to nonvisible sets after one-by-one addition and removal of items. J Comp Psychol 118:25–36

Beran MJ, Rumbaugh DM (2001) Constructive' enumeration by chimpanzees (*Pan troglodytes*) on a computerized task. Anim Cogn 4:81–89

Beran MJ, Rumbaugh DM, Savage-Rumbaugh ES (1998) Chimpanzee (*Pan troglodytes*) counting in a computerized testing paradigm. Psychol Rec 48:3–19

Biro D, Matsuzawa T (2001) Use of numerical symbols by the chimpanzee (*Pan troglodytes*): cardinals, ordinals, and the introduction of zero. Anim Cogn 4:93–199

Boysen ST, Berntson GG (1989) Numerical competence in a chimpanzee (*Pan troglodytes*). J Comp Psychol 103:23–31

Boysen ST Berntson GG, Hannan MB, Cacioppo JT (1996) Quantity-based interference and symbolic representations in chimpanzees (*Pan troglodytes*). J Exp Psychol Anim Behav Process 22:76–86

Boysen ST, Capaldi EJ (1993) The development of numerical competence: animal and human models. Erlbaum, Hillsdale, N.J.

Brannon EM, Terrace HS (1998) Ordering of the numerosities 1 to 9 by monkeys. Science 282:746–749

Brannon EM, Terrace HS (2000) Representation of the numerosities 1–9 by rhesus macaques (*Macaca mulatta*). J Exp Psychol Anim Behav Process 26:31–49

Chiang WC, Wynn K (2000) Infants' representation and tracking of multiple objects. Cognition 77:169–195

Clearfield MW, Mix KS (1999) Number versus contour length in infants' discrimination of small visual sets. Psychol Sci 1:408–411

Clearfield MW, Mix KS (2001) Amount versus number: infants' use of area and contour length to discriminate small sets. J Cogn Dev 2:243–260

Feigenson L, Carey S, Hauser MD (2002) The representations underlying infants' choice of more: object files versus analog magnitudes. Psychol Sci 13:150–156

Feigenson L, Carey S, Spelke E (2002) Infants' discrimination of number vs. continuous extent. Cogn Psychol 44:33–66

Flombaum JI, Junge JA, Hauser MD (2005) Rhesus monkeys (*Macaca mulatta*) spontaneously compute addition operations over large numbers. Cognition (in press)

Gallistel CR (1990) The organization of learning. MIT Press, Cambridge

Hauser MD (2000) Wild minds: what animals really think. Holt, New York

Hauser MD, Carey S (1998) Building a cognitive creature from a set of primitives: evolutionary and developmental insights. In: Allen C, Cummins D (ed) The evolution of mind. Oxford University Press, Oxford, pp 51–106

Hauser MD, Carey S (2003) Spontaneous representations of small numbers of objects by rhesus macaques: examinations of content and format. Cogn Psychol 47:367–401

Hauser MD, Carey S, Hauser LB (2000) Spontaneous number representation in semi-free-ranging rhesus monkeys. Proc R Soc Lond Biol Sci 267:829–833

Hauser MD, Dehaene S, Dehaene-Lambertz G, Patalano A (2002) Spontaneous number discrimination of multi-format auditory stimuli in cotton-top tamarins (*Saguinus oedipus*). Cognition 86:B23–B32

Hauser MD, MacNeilage P, Ware M (1996) Numerical representations in primates. Proc Natl Acad Sci 93:1514–1517

Hauser MD, Spelke ES (2004) Evolutionary and developmental foundations of human knowledge: a case study of mathematics. In: Gazzaniga M (ed) The cognitive neurosciences III. MIT Press, Cambridge, pp 853–864

Hauser MD, Tsao F, Garcia P, Spelke ES (2003) Evolutionary foundations of number: spontaneous representations of numerical magnitudes by cotton-top tamarins. Proc R Soc Lond B 270:1441–1446

Koechlin JD, Dehaene S, Mehler J (1997) Numerical transformations in five-month-old human infants. Math Cogn 3:89–104

Lewis KP, Jaffe S, Brannon E (2005) Analog number representations in mongoose lemurs (*Eulemur mongoz*): evidence from a search task. Anim Cogn DOI 10.1007/s10071-004-0251-x

Lipton JS, Spelke ES (2003) Origins of number sense: large-number discrimination in human infants. Psychol Sci 14:396–401

Matsuzawa T (1985) Use of numbers by a chimpanzee. Nature 315:57–59

Rumbaugh DM, Savage-Rumbaugh S, Hegel MT (1987) Summation in the chimpanzee (*Pan troglodytes*). J Exp Psychol Anim Behav Process 13:107–115

Rumbaugh DM, Washburn DA (1993) Counting by chimpanzees and ordinality judgments by macaques in video-formatted tasks. In: Boysen ST, Capaldi JE (ed) The development of numerical competence: animal and human models. Erlbaum, Hillsdale, pp 87–106

Santos LR, Sulkowski G, Spaepen GM, Hauser MD (2002) Object individuation using property/kind information in rhesus macaques (*Macaca mulatta*). Cognition 83:241–264

Simon T, Hespos S, Rochat P (1995) Do infants understand simple arithmetic? A replication of Wynn (1992). Cogn Dev 10:253–269

Spelke ES (2000) Core knowledge. Am Psychol 55:1233–1243

Tomasello M, Call J (1997) Primate cognition. Oxford University Press, New York

Uller C, Hauser M, Carey S (2001) Spontaneous representation of number in cotton-top tamarins (*Saguinus oedipus*). J Comp Psychol 115:248–257

Washburn DA, Rumbaugh DM (1991) Ordinal judgments of numerical symbols by macaques (*Macaca mulatta*). Psychol Sci 2:190–193

West RE, Young RJ (2002) Do domestic dogs show any evidence of being able to count? Anim Cogn 5:183–186

Wynn K (1992) Addition and subtraction by human infants. Nature 358:749–750

Wynn K, Bloom P, Chiang WC (2002) Enumeration of collective entities by 5-month-old infants. Cognition 83:B55–B62

Xu F (2003) Numerosity discrimination in infants: evidence for two systems of representations. Cognition 89:B15–B25

Xu F, Spelke ES (2000) Large number discrimination in 6-month olds. Cognition 74:B1–B11