

PAPER

Enumeration of objects and substances in non-human primates: experiments with brown lemurs (*Eulemur fulvus*)

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Abstract

Both human infants and adult non-human primates share the capacity to track small numbers of objects across time and occlusion. The question now facing developmental and comparative psychologists is whether similar mechanisms give rise to this capacity across the two populations. Here, we explore whether non-human primates' object tracking abilities are subject to the same constraints as that of human infants. In particular, we examine whether one primate species, the brown lemur (*Eulemur fulvus*), also fails to represent and enumerate objects when they behave non-rigidly or non-cohesively. We presented lemurs with a series of expectancy violation studies involving simple 1 + 1 addition events in which we varied the entities to be enumerated. Like infants, lemurs successfully enumerated the two objects when those objects were rigid cohesive individuals, but failed to enumerate similar-looking non-rigid piles of sand. In contrast to results with human infants, however, lemurs successfully enumerated non-cohesive objects that broke into multiple pieces. These results are discussed in light of recent theories about object processing in human infants and adults.

Introduction

The capacity to represent individual objects across time and occlusion is one of the most fundamental capacities in the human cognitive repertoire. Not surprisingly, psychologists have devoted tremendous empirical attention to the origins of our ability to represent objects. The developmental side of this work has demonstrated unambiguous evidence that preverbal infants can represent and track small sets of objects (see review in Feigenson, Dehaene & Spelke, 2004). Infants in the first year of life can enumerate small numbers of objects placed behind an occluder (e.g. Feigenson, Carey & Spelke, 2002b; Koechlin, Dehaene & Mehler, 1997; Simon, Hespos & Rochat, 1995; Wynn, 1992), track objects as they move behind occluders and into solid barriers (e.g. Aguiar & Baillargeon, 2002; Spelke, Kestenbaum, Simons & Wein, 1995) and recognize that objects retain their cohesive boundaries as they move in space (e.g. Chiang & Wynn, 2000; Spelke, Breinlinger, Macomber & Jacobson, 1992; Wynn, Bloom & Chiang, 2002).

¹ Note that infants do successfully discriminate and enumerate larger numbers in some tasks (e.g. Xu & Spelke, 2000). These successes, however, are commonly thought to require a different representational system, one that computes numerical information through the use of analogue magnitude representations (see Neider, 2005, and Feigenson *et al.*, 2004, for a discussion of this accumulator system for numerical representation).

Infants' impressive ability to track objects does, however, have some critical limits. One such limit concerns the number of objects that infants can keep track of at one time.¹ Infants' ability to keep track of hidden objects seems to break down when the number of objects involved exceeds three (see Feigenson & Carey, 2003; Feigenson, Carey & Hauser, 2002a; Starkey & Cooper, 1980). To take one striking example, Feigenson and colleagues (2002a) presented 12-month-olds with different numbers of graham crackers (rectangular-shaped children's cookies or biscuits) placed into small cups. Infants were then allowed to approach one of the cups, with the assumption that knowledgeable infants should spontaneously approach the cup that had the greatest number of crackers. Feigenson and colleagues observed that infants reliably enumerated the numbers of crackers inside the cups – approaching cups with two crackers over those with one and cups with three crackers over those with two. Remarkably, however, infants approached randomly whenever one cup had more than three crackers inside (i.e. comparisons of 3 vs. 4, 2 vs. 4, and 3 vs. 6). This failure to discriminate was especially striking when infants were presented with a cup containing one cracker and another containing four; here, infants again chose randomly even though the ratio between the sets of crackers in the two cups was four to one (Feigenson & Carey, 2005). These findings suggest that the set size of an array of objects poses a major limit on infants' object representation abilities.

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1 A different limitation on infants' object representation
 2 abilities concerns the *nature* of the individuals infants are
 3 representing. Infants seem to have more trouble
 4 representing individuals that don't behave as cohesive,
 5 rigid units (Huntley-Fenner, Carey & Solimando, 2002;
 6 Chiang & Wynn, 2000). Huntley-Fenner and colleagues
 7 (2002), for example, presented 8-month-old infants with
 8 occlusion events involving either rigid objects placed
 9 onto a stage or non-rigid piles of sand that were poured
 10 onto the stage. Although infants successfully enumerated
 11 the rigid objects, they failed to form any expectations
 12 about how many sand piles should be behind the stage.²
 13 Infants also seem to have trouble tracking non-cohesive
 14 objects – objects that break into smaller parts as they
 15 move in time and space; infants fail to notice when non-
 16 cohesive piles unexpectedly disappear, even though they
 17 easily detect such disappearances when they involve
 18 cohesive objects (Chiang & Wynn, 2000). Similarly,
 19 infants fail a version of the Feigenson *et al.* (2002a)
 20 cracker task in which the crackers broke before being
 21 placed into the cups, again suggesting that violations of
 22 cohesion disrupt infants' object representation abilities
 23 (Cherries, Mitroff, Wynn & Scholl, 2008). These results
 24 together suggest a second limit on infants' object
 25 tracking abilities – namely, they operate more poorly
 26 over both non-rigid and non-cohesive individuals.

27 Remarkably, these two limits on infants' object
 28 processing – the set size limit and the cohesive-rigid
 29 object constraint – seem to extend well beyond the first
 30 year of life and into adulthood. Vision researchers have
 31 observed that adults' capacity to represent multiple
 32 objects depends in part on the number of objects to be
 33 represented, with a common limit of four total objects
 34 (e.g. Cowan, 2001). More recent work has demonstrated
 35 that adults, like young infants, have trouble tracking
 36 objects that behave non-rigidly (vanMarle & Scholl,
 37 2003) and suffer more subtle processing constraints when
 38 objects behave non-cohesively (Mitroff, Scholl & Wynn,
 39 2004). The fact that infants and adults share the same
 40 limits on object processing has led to the view that
 41 human object representations are subserved by a set of
 42 developmentally stable mechanisms, ones that begin
 43 operating early in infancy and continue on into
 44 adulthood (see Feigenson *et al.*, 2004; Hauser &
 45 Spelke, 2004; Santos, 2004; Scholl & Leslie, 1999).

46 Although much is known about the developmental
 47 origins of human object tracking capacities, somewhat less
 48 is known about the evolutionary origins of these abilities.

49
 50 ² There is some evidence that infants do not perform poorly
 51 quantifying *all* forms of continuous substances. Gao and colleagues
 52 (2000), for example, observed that infants can quantify the amount of a
 53 substance inside a container. Similarly, vanMarle (2004) observed that
 54 infants can discriminate different portions of cheerios poured into cups
 55 when the quantity of those portions differ by a 1:4 ratio (5 cheerios
 56 versus 20 cheerios). Importantly, however, it is not clear that infants
 succeed on these two tasks through the use of object representations *per se*. Instead, it seems that infants again use a magnitude representational system to succeed in quantifying continuous quantities.

Nevertheless, recent research with our closest living evolutionary relatives – the non-human primates (hereafter primates) – has demonstrated that they too can track small sets of items across time and occlusion. Comparative researchers using experimental methods identical to those of developmental researchers have revealed that primates represent occluded objects about as well as human infants – primates recognize that objects persist while occluded (e.g. Flombaum, Junge & Hauser, 2005; Hauser, MacNeilage & Ware, 1996; Santos, Barnes & Mahajan, 2005; Uller, Hauser & Carey, 2001), trace continuous paths in space and time (Santos & Hauser, 2002; Santos, Seelig & Hauser, 2006), and retain cohesive boundaries as they move (Munakata, Santos, O'Reilly, Hauser & Spelke, 2001). The similarity with which humans and primates reason about objects has led some scholars to speculate that the same cognitive mechanisms underlie object processing across the primate order (see Feigenson *et al.*, 2004; Hauser & Spelke, 2004; Santos, 2004). If this is the case, then primates' object tracking abilities should be subject to the same processing constraints as have been observed in humans.

There is limited evidence that primates experience some of these object processing constraints – a limit on the number of objects that can be represented. After watching as solid food items (Hauser, Carey & Hauser, 2000) were placed into two buckets, rhesus monkeys (*Macaca mulatta*), like human infants, spontaneously searched the bucket with the larger number of apples, but only up to a limit of four apples. This set size limit of four objects has also been observed with solid objects using a looking time methodology (see Flombaum, Junge, Santos & Hauser, in preparation; Hauser & Carey, 2003). These results together suggest that primates, like humans, may be limited in the number of objects that they can successfully represent at any one time.

Although there is evidence that primates may share the set size limit that constrains human object tracking, there has to date been less investigation on whether primate object representations bear the second limit that constrains human object processing mechanisms – namely, that these mechanisms operate best over rigid, cohesive objects. Recently several investigators have explored whether primates' ability to enumerate sets of objects is impaired when the objects to be enumerated behave in non-rigid ways. vanMarle, Aw, McCrink and Santos (2006), for example, allowed capuchins (*Cebus apella*) to enumerate sets of objects that behaved either rigidly (i.e. sets of individual rigid raisins) or non-rigidly (sets of non-rigid banana smoothie) in a choice task similar to that used by Feigenson *et al.* (2002a) with human infants. Capuchins successfully enumerated sets of rigid and non-rigid entities equally well; monkeys discriminated between quantities of 1 vs. 4, 1 vs. 2, and 2 vs. 3 both for raisins and banana smoothie pours. Wood and colleagues (2008) found a similar pattern in rhesus macaques, who demonstrate the same set size limit when enumerating non-rigid 'pours' of carrot pieces

as they do when enumerating cohesive apple chunks. These findings raise the possibility that adult primates' object representations might differ from those of developing infants. Unfortunately, this conclusion seems premature for two reasons. First, to date no empirical study has tested primates and infants using exactly the same object stimuli, raising the possibility that purported group differences actually reflect differences in the methods or objects used in testing. Second, to date no research has explored whether primates can represent *non-cohesive* objects, ones that break apart during presentation.

Here, we extend previous work and examine how one primate species – the brown lemur (*Eulemur fulvus*) – represents individuals that behave non-rigidly and non-cohesively. Lemurs are prosimian primates, a distantly related suborder of primates that last shared a common ancestor with humans around 60 million years ago. Although brown lemurs are distant evolutionary relatives to humans, this species still appears to share the human capacity for enumerating small sets of objects (Santos *et al.*, 2005), and thus can serve as a good model for investigating the constraints that operate on primate object representations more generally.

In addition to extending this question to a new species, we also aim to use a different methodology for testing lemurs' capacity to enumerate different kinds of objects. Specifically, we examined how this species reasons about non-rigid and non-cohesive entities by presenting them with the same simple 1 + 1 addition event that has been used in many human infants studies (e.g. Feigenson *et al.*, 2002b; Hauser & Carey, 2003; Hauser *et al.*, 1996; Koechlin *et al.*, 1997; Santos *et al.*, 2005; Simon *et al.*, 1995; Uller *et al.*, 2001; Wynn, 1992). In this event, participants see two objects sequentially placed onto a stage behind a screen. When the screen is removed, one of two test events is revealed: either a possible outcome of two objects or an impossible outcome of only one object. Previous work has shown that lemurs look reliably longer at unexpected outcomes in this task (Santos *et al.*, 2005). In the present study, we first replicate this finding using two rigid, cohesive objects (Experiment 1). We then explore the roles of rigidity (Experiment 2) and cohesion (Experiment 3) by selectively varying these features and examining how these changes affect subjects' performance.

Experiment 1: Rigid, cohesive objects

Methods

Subjects

We tested 14 brown lemurs. All individuals live at the Lemur Conservation Foundation Reserve in Myakka City, Florida (see Table 1). The lemurs each inhabit one of two 13-acre forest enclosures, but were isolated in outdoor enclosures (1.0 m × 3.9 m × 2.2 m) for testing. The same lemurs participated in Experiments 2 and 3

(with approximately 24 hours between testing sessions), and experiment order was counterbalanced across subjects.

Materials and stimuli

Our looking time presentation involved two blue cone-shaped objects (12 cm in diameter at the base, 5 cm tall); objects were made from styrofoam balls carved into sand-pile shapes and then textured with glued blue sand; these cone objects physically resembled piles of blue sand in their shape, size, and material. The objects were presented on a black foamcore stage (51 cm × 18 cm × 18 cm), which was bisected by a small insert (18 cm × 24 cm × 0.4 cm), delineating the left and right sides of the stage, even when the stage was occluded (see Figure 1a). We used a screen (46 cm × 33 cm × 10 cm) with a hidden shelf on the back to block the stage and the stimuli from the subject's view.

Procedure

Once subjects were isolated in their enclosure, two experimenters entered an adjacent enclosure; the experimenters performed testing inside this enclosure to prevent interference from other free-ranging animals during the testing sequence. Both experimenters were familiar to the lemurs. The first experimenter presented displays to the subject while the second experimenter videotaped the trial.

Each session consisted of two baseline trials and then two test trials presented in a counterbalanced order. Baseline trials began when the presenter attracted subjects' attention and then lifted the screen to reveal either one object (the *one object baseline*) or two objects (the *two objects baseline*) sitting on the stage. The presenter then called 'Now', and the subjects' looking was recorded for 10 seconds. After baseline trials, subjects were presented with two test trials involving a 1 + 1 event (Santos *et al.*, 2005). The presenter began both test trials by presenting the subject with the empty stage. The presenter then held up a sand object, placed it in the center of the left side of the stage and then placed the screen in front of the stage, blocking it from the subject's view. Subsequently, she held

Table 1 Information on subjects tested across the three experimental conditions

Subject	Sex	Subspecies
Akako	M	<i>Eulemur fulvus rufus</i>
Bao	F	<i>Eulemur sanfordi</i>
Gideon	M	<i>Eulemur fulvus albifrons</i>
Fred	M	<i>Eulemur fulvus albifrons</i>
Ikoto	M	<i>Eulemur sanfordi</i>
Malbec	M	<i>Eulemur fulvus fulvus</i>
Mbola	F	<i>Eulemur sanfordi</i>
Pinot	M	<i>Eulemur fulvus fulvus</i>
Redlake	F	<i>Eulemur fulvus rufus</i>
Redwing	M	<i>Eulemur fulvus rufus</i>
Redwood	F	<i>Eulemur fulvus rufus</i>
Shiraz	F	<i>Eulemur fulvus fulvus</i>
Strawberry	F	<i>Eulemur fulvus rufus</i>
Tiana	F	<i>Eulemur sanfordi</i>

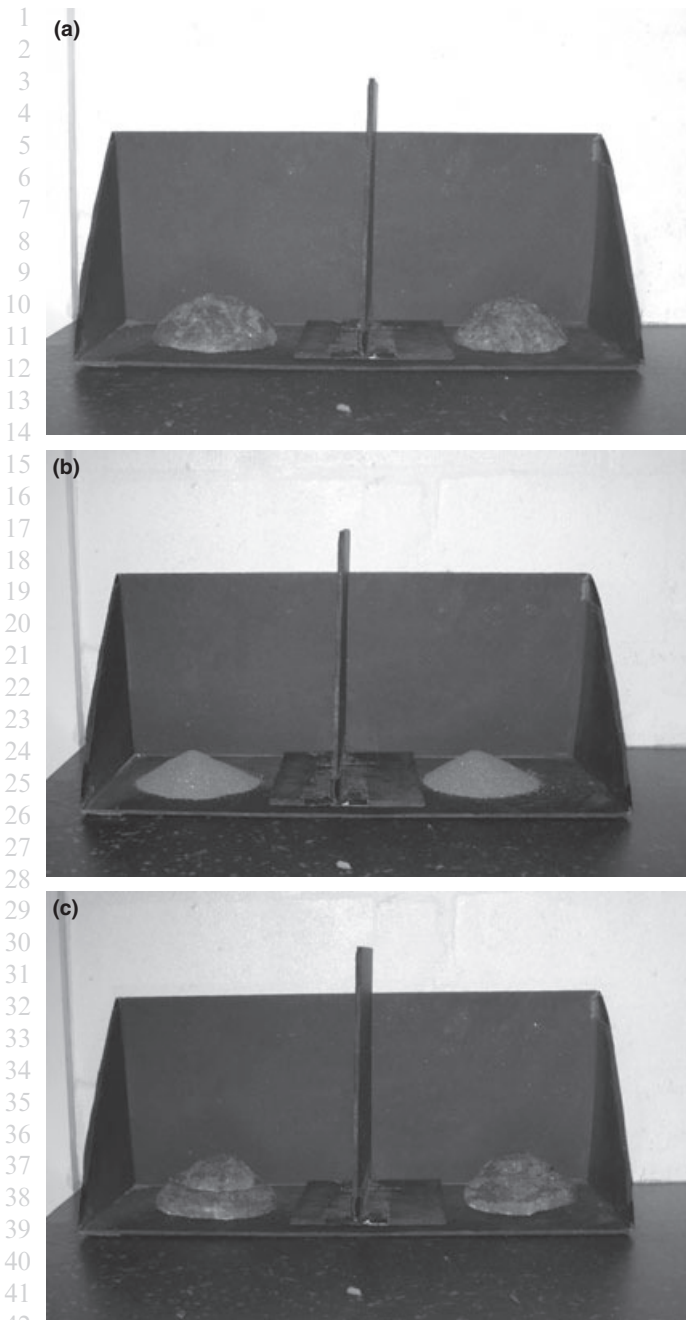


Figure 1 A photograph of the stimuli used in these studies. (a) Rigid cohesive stimuli used in Experiment 1. (b) Non-rigid stimuli used in Experiment 2. (c) Non-cohesive stimuli used in Experiment 3.

up a second sand object, placed it behind the screen in the center of the right side of the stage (either directly onto the stage or surreptitiously into the shelf attached to the screen), and then removed the screen to reveal one of two test outcomes (see Figure 2a): an expected outcome of two objects on the stage (the *two objects test*) or an unexpected outcome of only one object on the stage (the *one object test*). Immediately upon lifting the screen, the experimenter called 'Now', and looking was recorded for ten seconds.

Coding and data analysis

Tapes were digitized using iMovie and then analyzed with Quicktime software. A single coder who was blind to the experimental condition analyzed looking. A subset of trials ($n = 6$ lemurs) was scored by a second blind coder to establish reliability ($r = 0.85$).

Results

We observed no difference in looking across the two baseline trials ($t(13) = 0.50$, $p = .63$). Lemurs looked equally across one object (Mean = 3.93 s) and two object (3.60 s) baseline trials. Lemurs did, however, show a reliable preference during the test trials ($t(13) = 4.57$, $p = .0005$). Lemurs looked longer at the one object test trial (4.79 s) than at the two object test trial (2.53 s, see Figure 3a). This pattern of looking longer at the one object test trial was confirmed using non-parametric tests as well (Wilcoxon signed rank: $Z = 3.11$, $p = .002$).

Discussion

When presented with a 1 + 1 addition event involving rigid, cohesive objects, lemurs looked longer at an incorrect outcome of one object than at a correct outcome of two objects. This pattern of results coincides with those of previous studies suggesting primates can successfully track addition events involving small numbers of objects and additionally demonstrates that lemurs can successfully enumerate the blue sand objects in our task, at least when they behave rigidly and cohesively. Our next step was to explore the role of each of these two features—rigidity and cohesion—in lemurs' ability to track objects. We first altered the objects' rigidity, turning them from sand objects into sand *piles*, portions of sand that can be poured onto the stage (see Huntley-Fenner *et al.*, 2002, for a similar experiment with human infants). The two piles of blue sand used in Experiment 2 look similar to the sand object stimuli presented in Experiment 1. However, these piles moved to the stage not through a rigid motion, but instead through the non-rigid action of pouring. If lemurs' object tracking abilities are subject to the same constraints as those of human adults and infants, then subjects should fail to enumerate two piles of sand in this 1 + 1 event, looking equally at the two test outcomes.

Experiment 2: Non-rigid objects

Methods

Materials and stimuli

We used an experimental set-up identical to that of Experiment 1 except that our stimuli consisted of piles of blue sand that could be poured onto the stage. In their static state, these 'piles' of poured sand resembled the objects used in Experiment 1 (see Figure 1b). The sand was poured onto the stage using two separate clear plastic drinking cups.

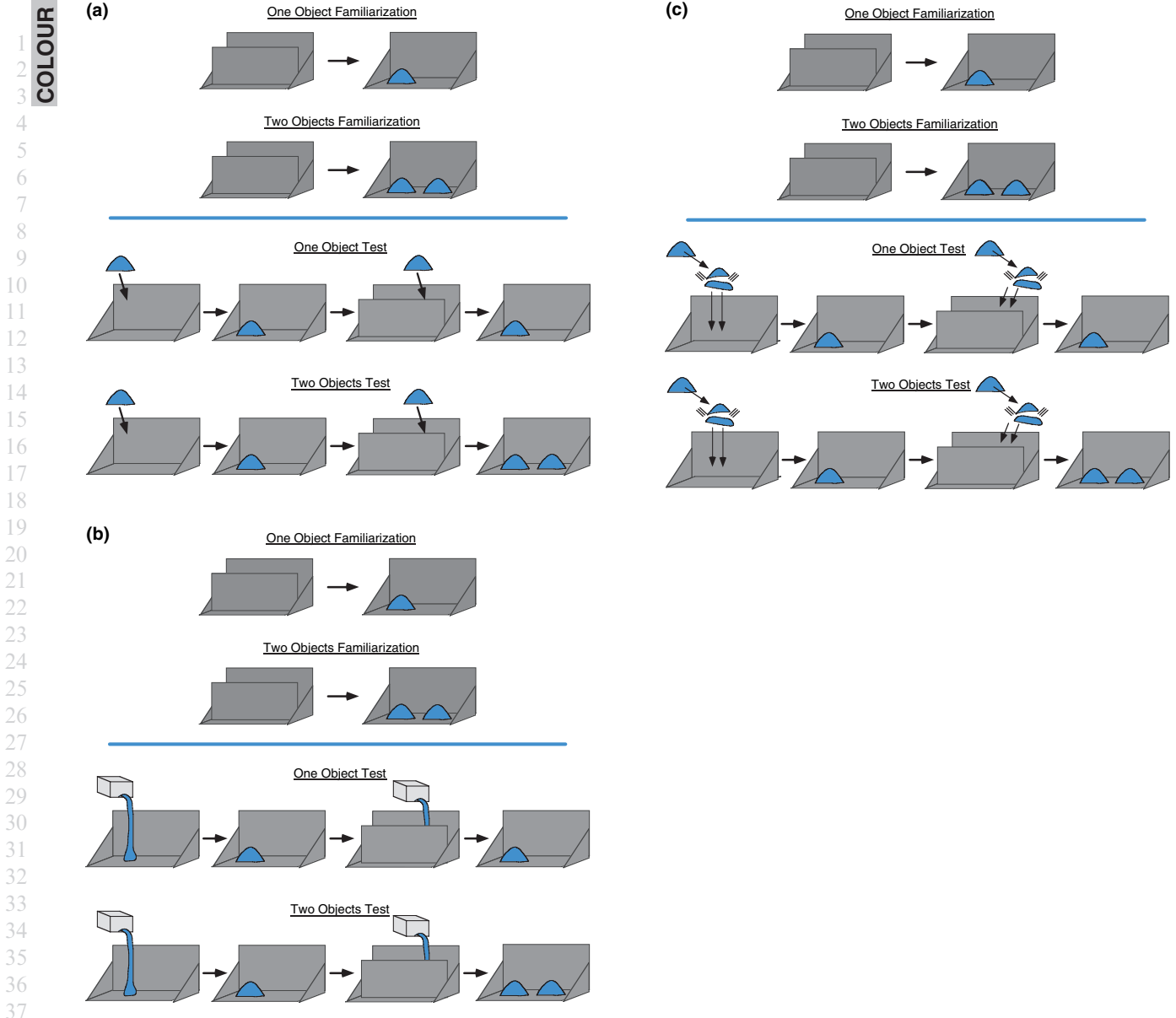


Figure 2 Familiarization and test events used in each experiment study. (a) Experiment 1. (b) Experiment 2. (c) Experiment 3.

Procedure

We used the same procedure as in Experiment 1 with the exception of the two test trial events. In Experiment 2 test trials, the experimenter began by presenting the subject with the empty stage, and then held up a cup filled with enough sand to form a pile approximately 12 cm in diameter and 5 cm in height. While the subject watched, the experimenter poured the sand onto the center of the left side of the stage into a cone shaped pile, visually similar in size and shape to the object seen in Experiment 1. She then occluded the stage with the screen, held a second cup (containing the same amount of sand) up over the screen and, while the subject was watching, poured the sand behind the screen onto the center of the right side of the stage (see Figure 2b). The presenter then lifted the screen to reveal either one or two piles of sand on the stage.

Results

We observed no difference in looking across the two baseline trials ($t(13) = 1.13, p = .28$) or test trials ($t(13) = 0.58, p = .57$). Lemurs looked equally at the one object (4.09 s) and two object baselines (4.70 s) as well as the one object (4.28 s) and two object test trials (3.89 s) (see Figure 3b). Non-parametric tests also revealed no difference across test trials ($Z = 0.91, p = .36$). We then performed a repeated measures ANOVA with experiment (1, 2) and test condition (1 object or 2 objects) as factors. We observed no main effect of experiment ($F(1, 26) = 0.63, p = .43$). We observed a significant main effect of test condition ($F(1, 26) = 10.16, p = .004$). Importantly, we observed a significant interaction between experiment and test outcome ($F(1, 26) = 5.12, p = .03$), suggesting that

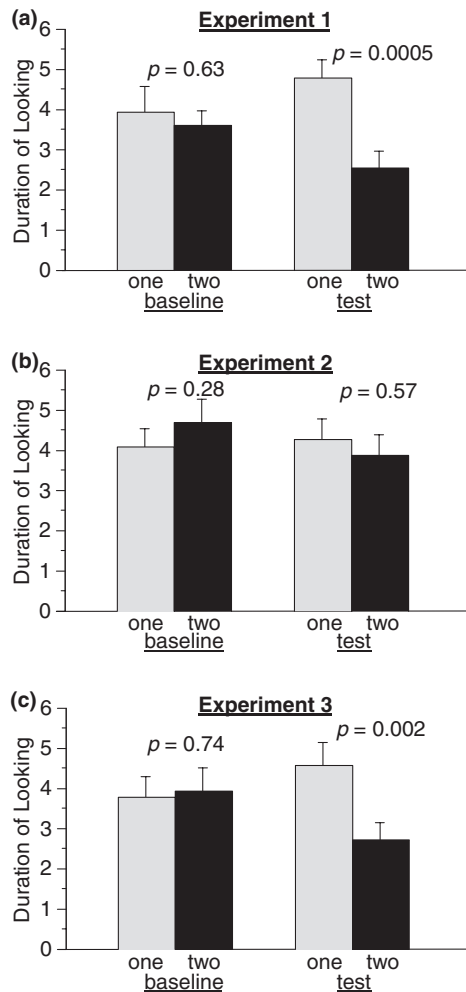


Figure 3 Duration of looking in seconds (mean \pm standard error) across familiarization and test trials. (a) Experiment 1. (b) Experiment 2. (c) Experiment 3.

lemurs showed significantly different patterns of performance across Experiments 1 and 2.

Discussion

In contrast to their performance with rigid objects, lemurs looked equally at a correct outcome of two piles and an incorrect outcome of only one pile. Although lemurs readily form accurate expectations about addition events involving rigid objects, they fail to make similar expectations when these events involve non-rigid piles of sand. Like human infants, lemurs appear to have problems representing objects that move in non-rigid ways. In the next study, we explore whether these similar problems also extend to non-cohesive objects. In Experiment 3, lemurs were required to enumerate blue sand objects that broke into two halves before they were placed onto the stage. Such violations of cohesion seem to disrupt humans' ability to represent objects (Chiang & Wynn, 2000; Mitroff *et al.*, 2004; Scholl & Pylshyn, 1999). If cohesion is also a critical constraint in lemurs'

object processing, we would expect that subjects should fail to enumerate objects that break into multiple parts before being placed onto the stage.

Experiment 3: Non-cohesive objects

Methods

Materials and stimuli

Stimuli consisted of blue sand pile objects identical to those of Experiment 1 except with a horizontal split in the center of the object. This split allowed the object to break into a top piece and a bottom piece. In this way, the split pile objects were perceptually similar to those of Experiments 1 and 2 when statically sitting on the stage (see Figure 1c), but could be placed onto the stage through a non-cohesive act of breaking.

Procedure

Experiment 3 proceeded as Experiment 1, except for the test events. In Experiment 3 test trials, the experimenter began by holding up an apparently whole sand object and, while the subject was watching, broke it into a top piece and a bottom piece. After breaking the object, the experimenter placed the bottom half in the center of the left side of the stage, and then placed the top half on top of it, reforming the original whole-looking sand object. The experimenter then placed the screen in front of the object such that it blocked both the object and the rest of the stage from the subject's view, held up and broke a second sand object, and placed first the bottom half and then the top half behind the screen into the center of the right side of the stage (see Figure 2c). The experimenter then lifted the screen to reveal either one object test event or a two object test event.

Results

We observed no difference in looking across the two baseline trials ($t(13) = 0.34$, $p = .74$). Lemurs looked equally across one object (Mean = 3.78 s) and two object (3.95 s) baseline trials. We did, however, observe a reliable preference during the test trials ($t(13) = 3.78$, $p = .002$). Lemurs looked longer at the one object test trial (4.58 s) than at the two object test trial (2.72 s, see Figure 3c). Wilcoxon signed ranks confirmed this pattern ($Z = 3.05$, $p = .002$). We then performed a repeated measures ANOVA with experiment (1, 3) and test condition (1 object or 2 objects) as factors. We observed no main effect of experiment ($F(1, 26) = 0.0004$, $p = .98$). We observed a significant main effect of test condition ($F(1, 26) = 34.94$, $p < .0001$). Importantly, we observed no interaction between experiment and test outcome ($F(1, 26) = 0.32$, $p = .57$). Lemurs' pattern of performance across test conditions was similar in Experiments 1 and 3.

Discussion

In contrast to their performance with non-rigid objects, lemurs looked reliably longer at an unexpected addition outcome of one non-cohesive object than an expected outcome of two non-cohesive objects. Lemurs therefore appear to represent the actions of non-cohesive objects in much the same way as they represent cohesive ones – they spontaneously track and enumerate non-cohesive objects across time and occlusion. This result differs from what one would predict based on the performance of human infants, who perform poorly in tasks in which they are required to represent non-cohesive objects (Chiang & Wynn, 2000; Cheries *et al.*, 2008).

General discussion

The goal of the present study was to investigate whether brown lemurs' object representations are subject to the same constraints as those of our own species, specifically those demonstrated by human infants tested in similar paradigms. At first glance, our results paint a somewhat confusing picture about the nature of primate object representations. On the one hand, lemurs' object tracking abilities seem to be much like those of infants – they fail to operate over non-rigid entities. Lemurs failed to enumerate two non-rigid sand piles in Experiment 2, even though they spontaneously enumerated similar looking sand *objects* in Experiment 1. This result suggests that lemurs may suffer the same constraints on object processing that sometimes plague human infants. To a lemur, the unit of object tracking may also be a rigid object, one that does not dynamically extend and contract as it moves across space (see vanMarle & Scholl, 2003). On the other hand, lemurs' object processing seems to differ from that of human infants. Lemurs succeeded in enumerating objects that broke (i.e. violated cohesion). This violation – an object splitting into two – seems to disrupt human infants' object processing (Chiang & Wynn, 2000; Cheries *et al.*, 2008), yet it failed to affect lemurs' ability to enumerate objects in Experiment 3.

Our pattern of findings also differs a bit from results observed in other studies to date exploring primate representations of non-rigid objects (e.g. vanMarle *et al.*, 2006; Wood *et al.*, 2008). Previous work has suggested that some primates can successfully enumerate sets involving 'pours' of banana smoothie (vanMarle *et al.*, 2006) or carrot pieces (Wood *et al.*, 2008), though in a within-subject design, they perform selectively worse when enumerating substances than when enumerating rigid objects (e.g. vanMarle *et al.*, 2006). It is also important to note, however, that both of these studies used non-rigid objects different from the one used in the present study, namely sand. Indeed, sand may provide the most stringent test case of limiting object representations, because one could view sand not *only* as a non-rigid substance, but also as non-cohesive. During our pouring events, different

streams of sand might 'break off' the main stream (see also Huntley-Fenner *et al.*, 2002), which probably did not occur in the case of banana smoothie pours (see vanMarle *et al.*, 2006). This issue raises the possibility that lemurs' failure to enumerate in Experiment 2 was based largely on the particular non-cohesive stimulus used. A second distinction between the current study and previous work concerns the nature of the task used. Previous studies demonstrating successful discrimination of non-rigid stimuli used a choice method involving different quantities of non-rigid foods (vanMarle, 2004; vanMarle *et al.*, 2006; Wood *et al.*, 2008). Our study, in contrast, involved an expectancy violation method in which our dependent measure of discrimination involved differences in duration of looking. It is possible that at least some of the differences in primates' performance across these studies concern the methodology used. Indeed, the same differences across methodologies are seen in human infant studies, with infants sometimes showing poorer enumeration of non-rigid substances in looking tasks (e.g. Huntley-Fenner *et al.*, 2002) than choice tasks (e.g. vanMarle, 2004). A final difference between our study and previous ones involves the kind of object used as a non-rigid stimulus. Previous work showing primates' successful discrimination of non-rigid objects involved food substances (banana smoothie in vanMarle *et al.*, 2006 and carrot pieces in Wood *et al.*, 2008). It is possible that primates are more motivated to enumerate food objects, which may have led them to succeed in other tasks. Future work could therefore profit from testing lemurs with discriminations of non-rigid food substances to see if their performance might improve when foods are used as stimuli.

The pattern of results in the current study, however, suggests that primate (or at least, lemur) object representations may differ from those of human infants in that they are more bound to the rigidity of the units involved than to their cohesion. Although these results differ to some extent from what we might have expected based on the human infant pattern of results, they do fit with more subtle aspects of the pattern observed in older human participants, adults tested in mid-level vision studies. Adult human object representations, like those of lemurs, seem to be more negatively affected by violations of rigidity (i.e. objects that act as substances) than violations of cohesion (i.e. rigid objects that break). vanMarle and Scholl (2003), for example, found that adult participants tested in a multiple object tracking (MOT) task (see Pylyshyn & Storm, 1988) failed to track objects that behaved as substances (Experiment 1), but had no difficulty tracking 'non-cohesive' groups of objects (Experiment 2b). Similarly, Mitroff and colleagues (2004) examined whether cohesion violations disrupt subjects' performance in an object-reviewing task (see Kahneman, Treisman & Gibbs, 1992). Mitroff and colleagues found that subjects still experience an object-specific priming benefit in this task when the objects involved violation cohesion by splitting into two, just as

1 our sand objects did in Experiment 3. Although these non-
 2 cohesive priming benefits were reliably smaller than those
 3 resulting from cohesive objects, the fact that *any* object-
 4 specific benefit remains after a cohesion violation suggests
 5 that an adult's representation of an object can survive even
 6 after that object has split in half. Taken together, then,
 7 adult humans tested in MOT and object-reviewing tasks
 8 seem to treat objects in much the same way as lemurs did in
 9 our enumeration task – they can represent objects that
 10 move non-cohesively, but fail to represent objects that
 11 extend and contract like substances.

12 Note, however, that adult human performance was not
 13 totally unaffected by violations of cohesion. As Mitroff
 14 and colleagues (2004) observed, cohesion violations seem
 15 to take their toll on object representations in more subtle
 16 ways (by decreasing the magnitude of priming benefits,
 17 etc.). It would therefore be interesting to see whether
 18 cohesion violations disrupt lemur object representations
 19 in similarly subtle ways, leading to either increased
 20 reaction times and/or greater processing demands. It is
 21 also possible that increasing the non-cohesiveness of the
 22 objects (e.g. breaking them into more than two pieces)
 23 would make the task more difficult for lemurs. Future
 24 experiments with lemurs and other primates could
 25 therefore profit from designing more sensitive measures
 26 which, like the object-reviewing paradigm, can access
 27 more subtle changes in primates' performance across
 28 conditions.

29 The similarity with which adult lemurs and humans
 30 deal with various object violations leads to an important
 31 developmental prediction about human object
 32 processing, one that concerns human infants' problems
 33 enumerating non-cohesive objects (e.g. Chiang & Wynn,
 34 2000; Cheries *et al.*, 2008). The fact that adult lemurs
 35 successfully enumerate objects that undergo cohesion,
 36 but not rigidity violations, suggests that the features of
 37 rigidity and cohesion may affect the construction and
 38 maintenance of object representations in importantly
 39 different ways. Such a difference may play itself out
 40 developmentally, with infants acquiring the capacity to
 41 enumerate non-cohesive objects before they develop the
 42 same capacity for substance-like objects. Developmental
 43 psychologists may therefore profit from exploring when
 44 and how infants develop the capacity to represent objects
 45 that undergo cohesion violations. Such work on cohesion
 46 violations may provide important insight into the criteria
 47 that the visual system uses to determine when to activate
 48 or deactivate persisting object representations.

49 The goal of the present work was to explore whether
 50 lemurs share the same constraints on object processing
 51 that affect human infants. Our work provides the first
 52 evidence that, in addition to their set-size limitation (see
 53 Hauser *et al.*, 2000), some primates may also share a
 54 second constraint on object processing – they may have
 55 difficulty enumerating objects that behave in non-rigid,
 56 substance-like ways. In doing so, our work provides
 additional support for the view that humans and primates
 represent objects using similar (possibly homologous)

cognitive mechanisms, ones that suffer similar processing
 constraints. The present study also evidences how work
 with primates can further complement the increasingly
 profitable collaboration among adult and infant research-
 ers interested in the nature of object representations.
 Others have previously noted that research in adult vision
 can contribute to work in infant development (see
 vanMarle & Scholl, 2003; Mitroff *et al.*, 2004). We hope
 that work in primates can provide yet another empirical
 avenue for developing hypotheses about the mechanisms
 underlying and constraints on infants' representations of
 persisting objects.

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