

How Capuchin Monkeys (*Cebus apella*) Quantify Objects and Substances

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Humans and nonhuman animals appear to share a capacity for nonverbal quantity representations. But what are the limits of these abilities? Previous research with human infants suggests that the ontological status of an entity as an “object” or a “substance” affects infants’ ability to quantify it. We ask whether the same is true for another primate species—the new world monkey *Cebus apella*. We tested capuchin monkeys’ ability to select the greater of two quantities of either discrete objects or a nonsolid substance. Participants performed above chance with both objects (Experiment 1) and substances (Experiment 2); in both cases, the observed performance was ratio-dependent. This suggests that capuchins quantify objects and substances similarly and do so via analog magnitude representations.

A wealth of research on numerical cognition suggests that both human and nonhuman animals represent quantity nonverbally and use this information to guide their behavior. Preverbal human infants, for example, reliably reason about numerical information in a variety of different tasks (see Feigenson, Dehaene, & Spelke, 2004 and Gallistel & Gelman, 2005 for review).

Similarly, numerical abilities have been documented in a wide range of non-linguistic species such as rats, pigeons, parrots, raccoons, ferrets, lemurs, monkeys, and apes (see Brannon & Roitman, 2003; Davis & Perusse, 1988; Dehaene, 1997; Gallistel & Gelman, 2000; and Nieder, 2005 for review).

These nonverbal numerical abilities are quite general. Both human and nonhuman animals represent numerical information regardless of whether the stimuli involve auditory or visual events (e.g., Hauser, Tsao, Garcia & Spelke, 2003; Jordan, Brannon, Logothetis, & Ghazanfar, 2005; McCrink & Wynn, 2004; Meck & Church, 1983; Whalen, Gallistel, & Gelman, 1999), objects in the world (e.g., Hauser, MacNeilage, & Ware, 1996; Wynn, 1992), or actions produced by the animal (e.g., lever presses, Fernandes & Church, 1982; Mechner, 1958). In addition, rhesus macaques (*Macaca mulatta*) and capuchin monkeys (*Cebus apella*) can order pairs of stimuli on the basis of numerosity (Brannon & Terrace, 1998; 2000; Judge,

This research was supported by Yale University. This work was approved by the Yale University IACUC committee and conforms to federal guidelines for the use of animals in research.

The authors would like to thank Miriam Bowring, Laura Edwards, Bryan Galipeau, Heidi Hansberry, Nathan Herring, Iris Ma, Samantha Santos, Adena Schachner, and Brandon Schneider for their help in running these studies. We are grateful to Rochel Gelman, Daniel Gottlieb, and three anonymous reviewers for helpful comments on earlier versions of this manuscript.

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Evans, & Nyas, 2005). Infants and some animal species have also been observed to perform mental computations over their number representations (e.g., Boysen & Berntson, 1989; Call, 2000; Wynn, 1992). Preverbal infants, for example, have been shown to discriminate between correct and incorrect numerical results of large number addition and subtraction events shown on a computer screen (i.e., $5 + 5$ or $10 - 5 = 5$ or 10 ; McCrink & Wynn, 2004). Similarly, Brannon, Wusthoff, Gallistel, & Gibbon (2001) found that pigeons can be trained to make a behavioral response on the basis of a comparison made between a standard number and the number resulting from a numerical subtraction. Additionally, human infants, chimpanzees and rhesus monkeys who observe an experimenter sequentially hide different numbers of food items in two different boxes will preferentially approach the box containing the larger total number (Beran, 2001, 2004; Feigenson, Carey, & Hauser, 2002; Hauser, Carey, & Hauser, 2000).

Much debate has surrounded the nature of the representations underlying this nonverbal number capacity. Over the past few decades, researchers have proposed several types of mechanisms for representing number. One prominent class of models includes those in which quantity is represented via analog magnitudes. Although these models come different flavors (e.g., “accumulator model”, Meck & Church, 1983; “neural filtering model”, Dehaene & Changeaux, 1993¹), the

signature property of all analog magnitude models is that the discriminability of two values depends on their proportionate difference (i.e., ratio), rather than their absolute difference. Thus, it should be easier to discriminate 4 from 8, than 8 from 12, even though the values differ by the same number of units in both cases. To date, a great deal of evidence has been gathered in support of analog magnitude models. Researchers have observed ratio-dependent performance in a variety of nonhuman animal species (e.g., Beran, 2001, 2004; Beran & Beran, 2004; Beran & Rumbaugh, 2001; Lewis, Jaffe, & Brannon, 2005; Mechner, 1958; Meck & Church, 1983; Nieder & Miller, 2004), as well as in infant and adult humans (e.g., Cordes, Gallistel, & Gelman, & Whalen, 2001; McCrink & Wynn, 2004; Xu & Spelke, 2000; Xu, Spelke, & Goddard, 2005).

Other researchers have proposed a different kind of model to explain numerical performance: the object tracking mechanism (e.g., Kahneman, Treisman, & Gibbs, 1992; Pylyshyn, 1989). Object tracking mechanisms are not mechanisms for number processing per se, but instead operate as a series of visual attention processes consisting of a limited number of indexes that “point” to individual objects in the world. Such pointers allow an organism to keep track of objects as they move through space and undergo occlusion. The signature property of this type of

¹ Recent research by Nieder, Freedman, and Miller (2002) and Nieder and Miller (2003) found single cells in the primate prefrontal cortex that are tuned to respond to specific numerosities. The activation of these cells can explain scalar variability in behavioral numerical discrimination data since the tuning curves become wider as the preferred numerosity becomes larger. According to Nieder and Miller (2004), aspects

of this research (finding parallel, rather than serial processing of numerosity) accord particularly well with Dehaene and Changeaux’s (1993) “neural filtering model” in comparison to Meck and Church’s (1983) “accumulator model”. It should be noted that although these cells fire for arrays of simultaneously presented items, it is unclear whether or not they respond to the numerosity of sequentially presented stimuli. Meck & Church’s (1983) accumulator model, however, can explain how numerosity might be represented for both simultaneous and sequentially presented stimuli.

mechanism is its limited capacity--it can only track as many objects as it has indexes. In adult humans, this limit appears to be about four indexes (Pylyshyn, 1989; Pylyshyn & Storm, 1988).

Interestingly, human infants and various animals seem abstract the numerosity of sets smaller than four objects with considerable precision. These findings have led some investigators to adopt an object tracking account of these numerical abilities (Feigenson et al., 2002; Hauser et al., 2000; Simon, 1997). For instance, Simon (1997) proposed that infants in Wynn's (1992) "addition/subtraction" task were not doing arithmetic (as Wynn had originally suggested), but rather were detecting violations of object physics (i.e., that objects cannot spontaneously appear or disappear). The task is as follows: in the addition condition, infants first see one object placed on a stage. A moment later, a screen is raised to hide the object and then a second object is brought onto the stage and placed behind the screen. Finally, the screen is removed to reveal either two objects (the correct number) or one object (an incorrect number). Infants in this situation look longer when the incorrect number of objects is revealed.

On Simon's (1997) and similar accounts, the object tracking system in this situation deploys an index for each object, such that it represents both objects as being 'behind the screen'. When the screen is removed, the active indexes are placed in one-to-one correspondence with the revealed set. A mismatch between the number of indexes currently deployed and the number of items visible is thought to account for the fact that infants, monkeys, and lemurs look longer at numerically incorrect compared to numerically correct outcomes in situations like this (Hauser et al., 1996; Santos, Barnes,

& Mahajan, 2005; Simon, 1997; Wynn, 1992).

Previous research with both infants and nonhuman primates has examined which of these two types of mechanisms--analog magnitude representations or object tracking mechanisms--underlies nonverbal number processing. Much of this work has sought to rule out one mechanism or the other as an explanation for animals' ability to respond on the basis of number. Recently however, a growing body of evidence has begun to support the idea that human and nonhuman animals may employ *both* of the proposed mechanisms for enumeration, albeit in different circumstances (see Flombaum, Junge, & Hauser, 2005; Hauser & Carey, 2003). The new objective for work in numerical cognition, then, is to examine the conditions under which one or both of the mechanisms are engaged in a given task and why, which in turn provides information about the nature and limits of each of the two mechanisms.

One recent proposal is that analog magnitudes and object indexes operate over different parts of the number range (e.g., Feigenson et al., 2004; Hauser & Spelke, 2004; Xu, 2003). Clearly, this could be true for the object tracking mechanism, which by definition is limited to representing small sets. A more striking proposal is that analog magnitudes represent *only* large values (i.e., more than four). Limited evidence for this comes from studies of infant numerical processing². For example, human infants fail to discriminate small values at a 1:2 ratio

²Note however, that evidence from human adults (Cordes et al., 2001) shows that the accumulator represents both large and small values. When asked to press a key the same number of times as a target value, there was a constant coefficient of variation within the distribution of responses across both the small (four or fewer) and large number ranges (five or more).

(e.g., 1 vs. 2 dots: Xu, 2003), even though they readily discriminate larger values at a 1:2 ratio (e.g., 8 vs. 16 dots: Xu, 2003; Xu & Spelke, 2000; Xu et al., 2005). Converging evidence comes from infants' performance in an ordinal choice task. When asked to choose between two hidden quantities of graham crackers, 10-month-old infants reliably chose the container with the larger amount (e.g., 2 crackers over 1³, 3 crackers over 2, see Feigenson et al., 2002). Performance fell to chance, however, whenever there were more than 3 crackers hidden in a given container (e.g., 3 vs. 4, 1 vs. 4). This was true even though the ratio between the quantities should have been large enough to allow infants to judge which container had more if analog magnitudes were being used (i.e., 1 vs. 4 crackers). To account for this 'set size signature', researchers concluded that infants use the object tracking system alone to track small sets of objects, and that in infants this mechanism is limited to tracking only 3 objects (Feigenson & Carey, 2003; Feigenson et al., 2002).

A second proposal concerning differences in the use of analog magnitudes and object indexes involves the nature of the *units* over which these two types of mechanisms operate. Previous research investigating object tracking processes in

adults suggests that this system might be limited to tracking rigid, cohesive objects (vanMarle & Scholl, 2003). Using a standard Multiple Object Tracking task (Pylyshyn & Storm, 1988), adults were asked to track 4 out of 8 identical items as they moved around a computer screen. When the items stopped moving, participants had to report which of the eight items were the original targets. Adults performed at ceiling when the items were rigid objects, but were near chance when the items were non-cohesive substances that "poured" from location to location. Taken together with studies showing that adults have difficulty tracking other non-object entities (e.g., parts, Scholl, Pylyshyn, & Feldman, 2001), this suggests that the natural units for this mechanism are bounded, cohesive objects.

The same limits appear to affect infants' tracking capacities. Infants can readily track small numbers of discrete objects, but not small numbers of nonsolid substances⁴ (i.e., piles of sand, Huntley-Fenner, 1995; Huntley-Fenner, Carey, & Solimando, 2002).

Specifically, using a modified paradigm based on Wynn's (1992) addition/subtraction task, Huntley-Fenner et al. (2002) compared infants' ability to track either rigid objects or nonsolid substances (i.e., piles of sand). Consistent with previous results, infants in this study looked reliably longer when 'one object' + 'one object' was shown to equal only 'one object' (a physically impossible and

³ Differential performance with small sets (failing to discriminate one vs. two in habituation studies, but successfully choosing two crackers over one in the ordinal choice task) can be explained by the fact that the relevant habituation studies (Xu, 2003; Xu & Spelke, 2000) controlled for continuous properties of the displays so that number was the only dimension available as a basis for discrimination. Studies using the ordinal choice task, in contrast, generally do not control for continuous properties such that they are confounded with number. Under these conditions, infants successfully discriminate between small values as long as the number of items in a set does not exceed three.

⁴ Throughout this paper, we shall use the term "substance" to refer exclusively to nonsolid substances such as sand or water, rather than solid substances such as wood or metal. This further distinction between solid and nonsolid substances is orthogonal to the contrast of interest here since solid substances, like wood, though they have no inherent form, maintain their form under movement, making them more like discrete objects than nonsolid substances.

numerically incorrect outcome). In contrast, when piles of sand were used instead of bounded, cohesive objects, infants looked equally long regardless of how many piles were revealed following the 1 + 1 operation. Thus, not only did they fail to notice that there were only “half as many” piles as there should have been, they also failed to notice that there was only “half as much” sand as there should have been.

Interestingly, however, infants can quantify substances under some circumstances. vanMarle (2004) tested 10- to 12-month-old infants’ ability to select the larger of two hidden quantities of either discrete objects (graham crackers) or portions of substance (Cheerios). The object condition involved the sequential lowering of individual crackers into two opaque cups. The substance condition differed in two ways that emphasized the substance-like nature of the Cheerios. First, each amount of Cheerios was presented on a plate as a single, bounded portion of stuff (i.e., the individual Cheerios were bunched together so that they formed a group with a single bounding contour). Second, each portion was poured into an opaque cup such that its non-cohesiveness was made salient. Results indicated that in the object condition, infants readily selected 2 crackers over 1 (replicating previous findings, Feigenson et al., 2002). In the substance condition, however, an interesting pattern emerged. Infants who were given a choice between two quantities of Cheerios that differed by a 1:2 ratio (10 v 20 Cheerios) performed at chance. In contrast, those given a choice between quantities differing by a 1:4 ratio (5 v 20 Cheerios) reliably chose the larger amount. Since the food in this case violated cohesion (a property known to disrupt visual tracking in human adults), and since the number of individual grains of cereal in each portion clearly exceeded the

proposed capacity limits of the object tracking mechanism, these data suggest that infants may be able to use analog magnitudes to represent and compare substance quantities (vanMarle, 2004)⁵. A different pattern emerged when infants were given a choice between small portions in which the number of individual Cheerios in each portion was within or just outside the set size limit. Specifically, infants reliably chose 2 Cheerios over 1 (as they had done with crackers), but performed near chance when given a choice between 1 and 4 Cheerios. This “set size signature” indicates that infants may have been using object indexes when faced with small portions of Cheerios and thus were treating the small portions very differently from the large portions where they succeeded at a 1:4 ratio, but not a 1:2 ratio (vanMarle, 2004).

So far, we have seen evidence suggesting that infants may use object indexes to track small numbers of objects, and analog magnitude representations to quantify large numbers and substances. But what about nonhuman animals? Interestingly, while there is a great deal of evidence supporting the use of analog magnitudes in both animals and humans, there is less evidence for the object tracking mechanism in nonhuman animals. This is partly because the idea of an object tracking mechanism was only recently borrowed to explain human infants’ and

⁵ The reader may be skeptical that infants were treating the Cheerios portions as substances rather than a large collection of objects. However, note that if they were construing them as objects, then they should have succeeded at a 1:2 ratio, which even much younger infants can discriminate (e.g., McCrink & Wynn, 2004; Xu & Spelke, 2000; Xu et al., 2005). The fact that they required a 1:4 ratio to succeed with large portions of Cheerios suggests that they were in fact construing them as portions of substance rather than as a large collection of discrete objects.

nonhuman animals' performance on tasks involving small numbers of objects. However, it is also the case that many studies with nonhuman animals reveal a ratio signature, rather than a set size signature, across both the small and large number ranges (e.g., Beran, 2001, 2004; Beran & Beran, 2004; Beran & Rumbaugh, 2001; Lewis et al., 2005; Nieder & Miller, 2004). For example, using a computer joystick, chimpanzees (*Pan troglodytes*) were asked to "collect dots" one at a time until they had reached the number indicated by an Arabic numeral displayed at the beginning of the trial (target numerals 1 through 7). The chimps were above chance with all values, and performance was consistent with analog representations of number; the larger the quantity to be matched, the worse the chimps performed (Beran & Rumbaugh, 2001). Similar results were obtained using a different task in which chimpanzees saw different numbers of M&M's sequentially placed into two cups. Here, chimpanzees chose the greater number of candies significantly more often than chance, even when it contained up to nine candies. Again, performance was ratio-dependent. As the proportional difference between the quantities increased, so did performance. The same was true when multiple sets of candies were hidden in the cups, such that the chimps had to perform addition in order to choose the quantity with the greatest total number of candies (Beran, 2001, 2004).

However suggestive, the chimpanzees in these studies received hundreds of trials and, consequently, may have been representing quantity differently than they would in the wild. One way to avoid this issue is to try and observe nonhuman animals' spontaneous number abilities. Hauser et al. (2000) did just this by giving free-ranging rhesus monkeys a choice between two hidden

quantities of discrete food items. Monkeys reliably chose the box containing the larger number of food items for a variety of comparisons including one vs. two, two vs. three, and three vs. four, but chose randomly when offered four vs. six, three vs. eight and four vs. eight. Hauser and colleagues argued that this set-size limit demonstrated that rhesus monkeys were using object indexes, rather than accumulator representations, to determine which container had the most food. Increasing the ratio between the quantities did not always increase performance. Although monkeys reliably chose five over three food items, they were at chance on discriminations of four vs. eight and three vs. eight, suggesting that monkeys, like infants, generally failed to use accumulator magnitudes representations in this tracking task, even for highly discriminable values in the large number range (Hauser et al., 2000).

At present, the Hauser et al. (2000) tracking task provides the only strong evidence to date that a nonhuman animal represents and discriminates between small numbers of objects using object indexes. Unfortunately, however, this study does not fully rule out the possibility that the monkeys were using analog magnitudes in this task. First, the design of these studies prevents them from providing information about what discrimination function obtains in this task; because each monkey was tested only once, there is no way to see if the rhesus monkey participants showed subtle differences in performance that depended on the ratio comparison. Moreover, since different animals participated in different conditions, meaningful comparisons cannot be made across conditions. The present study aims to address this issue by examining how another primate species, the capuchin monkey, performs in a similar ordinal choice task.

The present set of experiments was designed with three goals in mind. First, we were interested in documenting numerical abilities in another primate species which to date has largely been neglected in studies of numerical cognition. Second, we wanted to examine whether evidence for analog magnitudes could be revealed in a task similar to that used to test nonverbal numerical abilities in other nonhuman primates and human infants. Third, we wanted to test whether monkeys, like infants (vanMarle, 2004), are able to quantify substances in this task and if so, what type of mechanism underlies this ability.

To establish more sensitive measures than Hauser et al. (2000), we tested monkeys on multiple trials and in multiple conditions. Such a within-subject design allowed us to reveal potentially subtle differences in performance across different ratio comparisons and to make more meaningful comparisons across conditions. To minimize any effect of training, the monkeys were never trained on test conditions and were not given any feedback as to whether they had made an appropriate choice.

Our first experiment was designed to establish simply whether or not this species could choose the greater of two hidden quantities of food in an ordinal choice task. Experiment 2 then went on to explore whether capuchins can quantify non-object entities and if so, what mechanism may underlie this ability.

Experiment 1

Method

Participants. We tested 6 brown capuchin monkeys (*Cebus apella*). Capuchins are large New World primates (see Fragaszy, Visalberghi, & Fedigan, 2004 for an excellent survey of this species' ecology and behavior). Unlike other New World species,

capuchins are an extremely dexterous species and are known to be adept tool-users both in the wild and in captivity. Our participants were housed at the Comparative Cognition Laboratory at Yale University (New Haven, CT); participants were born in captivity either at the present facility or at the Living Links Center capuchin colony in Yerkes Regional Primate Research Center (Atlanta, GA). Our participant group consisted of three males (FL, AG, NN) and three females (HG, JM, MD) ranging in age from 3y4m to 9y1m, with a mean age of 6y5m at the time of testing. All animals were housed together in a large social enclosure filled with toys, swings, and natural branches. The ambient temperature in the main enclosure (and thus during testing) remained relatively stable and was approximately 85° F with 85% humidity. Animals had ad libitum access to water and were fed a diet of chow and fruits supplemented by the food treats they receive during testing. All participants had previously participated in experiments concerning physics, social cognition, and tool use; these experiments sometimes involved reaching for different numbers of objects, but never involved representing different numbers of occluded objects, as was required in the present study.

Materials. The experiments were conducted in a cubic enclosure (82.5 cm³) elevated 76 cm from the floor and attached to the main enclosure. The walls of the experimental enclosure were made of wire mesh. After entering the experimental enclosure, a Plexiglas door was closed behind the monkey. The panel facing the experimenter was made of wire mesh and included a platform on the inside of the enclosure (25.4 cm above the panel floor) on which the monkeys could stand (see Figure 1). The panel had two openings (5 cm high x 9 cm long), spaced such that the participants could reach through one, but not both, of the openings at the same time, (approximately 25 cm apart). Attached to this panel (on the outside of the experimental enclosure) was a square wooden frame (61 cm x 61 cm) with two sets of rails. These rails supported an acrylic tray (58.5 cm long x 30.5 cm wide) that served as a presentation platform. When the tray was placed on the lower rails, participants were able to view, but not reach the tray. When it was lifted to the upper rails, participants could easily reach the quantities on it through the hand holes.

To ensure that the quantities were presented in the same place on each trial and that they would be accessible through the hand holes in the panel, two white plastic plates (15.25 cm in diameter) were secured on the front half of the tray acting as place

markers. The plates were covered with grey duct tape so the food items placed on them would be visible. This also minimized any potential auditory cues made by the sound of the food items dropping onto the plates⁶. To facilitate comparison to subsequent experiments, two red plastic cups (~4" tall and 3" in diameter at the opening) were used to cover food items by placing them upside-down over the quantities. The monkeys could not see the food items once hidden.

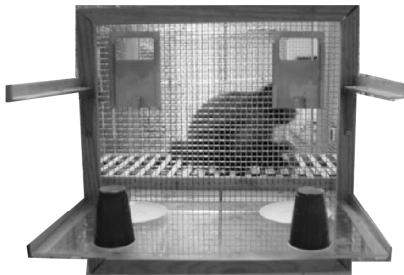


Figure 1. An experimenter's eye view of the testing chamber setup. The Plexiglas tray with two plastic plates serving as place markers was presented on the wood frame. The two red plastic cups were movable and used to occlude food items during presentations.

We used yogurt raisins⁷, a highly preferred food with which the participants had prior experience. Since successful performance in our task required selecting the larger of two amounts of food, we wanted to use highly desirable food items to increase the chance that the monkeys would attempt to obtain the larger amount. All test sessions were videotaped using a Sony Digital Handycam (DCR-TRV140).

⁶ In fact, it is highly unlikely that monkeys could have used the sound of food items dropping onto the plates for two additional reasons. First, our food items had a yogurt coating that softened within 2-3 minutes of being brought into the testing area due to the high heat and humidity, so that they made little sound upon landing on the plates. Additionally, since the testing took place inside the same room in which the monkeys were housed, there was a substantial amount of ambient noise (e.g., almost constant vocalizations of the monkeys, noise generated by monkeys leaping from swing to swing and climbing around the enclosure, etc.) that would have masked any potential noise made by the dropping of the raisins.

⁷ Yogurt raisins are raisins that have been coated in a creamy yogurt confection. They are a common snack food in the USA.

Design and Procedure. Participants were tested individually inside the experimental enclosure. At the beginning of each session, the participant entered the experimental enclosure for a food treat (a peanut). The experimenter then closed the Plexiglas panel behind the participant, securing them in the enclosure. This was done to ensure that the other monkeys could not interrupt the test participant.

Participants stood or seated themselves on the platform in the presentation area. Each session consisted of 10 test trials. At the start of each trial, the experimenter faced the monkey and placed the tray on the lower rails. The experimenter then tapped the cups on the tray to draw the monkey's attention and then placed them upside-down, one on each plate. Each cup had a small hole poked through the bottom so that the raisins could be dropped into them, but the monkey could not view the resulting quantity. Raisins were then dropped into a cup while the monkey watched. For each placement, the experimenter retrieved a single yogurt raisin from a small container, held it up to the participant, and then dropped it onto the plate through the hole, saying "Look" followed by the participants' name. To ensure the monkeys saw each placement, the experimenter did not place a yogurt raisin into the cup unless the monkey was attending to the event. Since it was not uncommon for monkeys to look away during the presentation, the amount of time it took to hide a particular number of raisins and the rate at which the raisins were hidden often varied. Thus, although 'duration of presentation' and 'rate of presentation' were generally confounded with 'number of items', they were at best only partially reliable cues. Nonetheless, it is possible that monkeys could have used these cues on some of the trials.

One quantity was presented first and then the other with the order (larger-first or smaller-first) counterbalanced across trials. Once all the raisins were dropped into the cups, the experimenter tapped the center of the tray frame until the monkey centered itself between the two hand-holes. Once the participant centered himself or herself, the experimenter immediately lifted the tray onto the upper rack, within reach of the participant. To avoid cuing the monkeys in any way, the experimenter always lifted the tray in the same manner and looked directly ahead (rather than at the tray or either of the two cups). Monkeys indicated their choice by reaching through one of the hand-holes, knocking over the cup and obtaining the raisins on that plate. After the participant obtained the selected quantity, the tray was immediately removed (out of the participants' reach) and replaced on the lower rack.

Finally, the unselected pile was uncovered, revealing the unselected quantity underneath, which was placed back into the original container. Participants were allowed only one choice per trial.

Because participants had never participated in a choice experiment of this nature before, we began with an *initial training condition* in which participants were given a choice between one raisin and zero raisins. This initial condition ensured that participants understood how to make choices and could easily displace the cups to obtain the yogurt raisins. Because the comparison was between one and zero raisins, participants were reinforced only when they made a correct choice; participants who mistakenly chose the plate with zero raisins received no food. Participants were required to achieve a criterion of 80% correct for two consecutive sessions in order to move on to the first test condition.

Once participants had completed this initial training condition, they received an *initial one vs. two test session* consisting of ten trials. In this test session, participants were presented with a choice between one raisin and two raisins. Because test sessions were aimed at exploring how participants responded to a particular comparison in the absence of training, participants were allowed to eat whichever quantity they chose. Thus, correct choices were differentially rewarded only to the extent that they provided double the amount of food as was obtained on the incorrect choices; wrong choices were penalized only in the sense that participants did not obtain the largest possible food reward.

After participants had completed this initial one vs. two test session, they continued on to *additional testing sessions*, each of which involved one of the three other numerical comparisons of interest—either one vs. four, two vs. three, and three vs. four. Again, each test session consisted of 10 trials. The order in which these three test sessions were presented was counterbalanced across monkeys. As in the initial one vs. two test session, participants were not differentially reinforced during these additional test sessions—participants received whichever pile of raisins they chose during test trials, even if this was the incorrect smaller amount.

Unfortunately, because both choices led to successful retrieval of some amount of food in these additional test sessions (i.e., incorrect choices were still rewarded), we worried that participants might begin to ignore the actual numerical comparisons and either resort to choosing randomly or develop side biases. To reduce the possibility of such alternative strategies, we

ran participants on *interim training sessions* in between all of these additional test sessions, ensuring they knew that the task was to always choose the larger amount. These interim training sessions presented participants with a choice of one vs. zero (the same comparison used in the initial training session). Note that participants only obtained the raisin when they correctly chose the larger amount of one raisin. As in the initial training conditions, participants were required to achieve a criterion of 80% correct for two consecutive sessions before moving on to the next test condition.

Results

All 6 participants performed at 100% across the first two sessions of their initial training phase, allowing them to continue onto the initial one vs. two test session. Participants performed above chance (Mean \pm SD = 75 \pm 14%) on this initial test condition; on average, all 6 monkeys chose two raisins over one raisin ($t(5) = 4.44, p < 0.003$).

Participants then moved onto the additional test conditions. Mean \pm SD percent correct was 85 \pm 10% (CI⁸ = 77-93%), 65 \pm 12% (CI = 55-75%), and 57 \pm 10% (CI = 48-65%) for one vs. four, two vs. three, and three vs. four, respectively (see Figure 2). T-tests compared performance on each comparison against chance performance (50%). Performance was significantly better than chance in the one vs. four condition ($t(5) = 8.17, p = 0.0002$) and the two vs. three condition ($t(5) = 3.00, p = 0.02$), but was only marginally above chance in the three vs. four condition ($t(5) = 1.58, p = 0.09$). We then performed a repeated measures ANOVA with condition (one vs. four, two vs. three, and three vs. four) as a within subject factor. We observed a significant effect of condition

⁸ All confidence intervals (CIs) reported in this paper were computed with 95% confidence limits.

($F(2,10) = 8.01, p = 0.008, \eta^2_G = 0.43^9$).

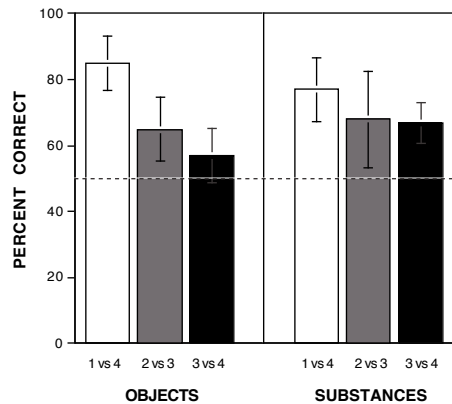


Figure 2. Mean percentage correct (including 95% confidence intervals) across different numerical comparisons in object (Experiment 1) and substance (Experiment 2) conditions.

Participants performed significantly differently across the three test comparisons, with highest performance on the discriminations involving the largest the ratio between the two quantities. Given the strong effect of condition, we wished to further explore the hypothesis that performance in the test conditions was ratio-dependent. To do so,

⁹ As a measure of effect size, we used η^2_G (generalized eta squared). To give the reader a sense of how this measure should be interpreted, consider it just like any other correlation coefficient--it signifies what proportion of the variation can be accounted for by the independent variable (Howell, 1997). For example, if $\eta^2_G = .43$, as it does for the effect of ratio condition in the Experiment 1, then 43% of the variation in performance was attributable to the ratio condition. This measure is recommended over *eta squared* and *partial eta squared* for effects obtained in analyses with repeated measures because *eta squared* and *partial eta squared* can give biased estimates of the effect size that are larger than would be obtained in the same study using a between subjects design (Olejnik & Algina, 2003). This would defeat the purpose of providing effect size measures in the first place since it would prevent one from comparing effect sizes across similar studies using different designs.

we performed a correlation between the ratio presented (expressed as the proportional similarity between the two numbers presented: one vs. four = 25%, two vs. three = 67%, and three vs. four = 75%) and participants' performance. We observed a robust negative correlation of $r = -0.75, t(16) = 4.60, p < 0.0003$; as the proportional similarity between the numbers increased, participants' performance decreased.

Non-parametric tests revealed a similar pattern. We used a binomial test to measure the reliability of each monkey's performance in each test condition (one v four, two v three, and three v four--see Figure 3). Results revealed that the number of monkeys reliably choosing the larger amount for the one v four, two v three, and three v four comparisons, respectively, was 5/6, 2/6, 0/6. Thus, despite substantial individual differences, monkeys' performance again appeared to be ratio-dependent. Monkeys' performance was better the large the proportional difference between the amounts.

Discussion

Like chimpanzees (Beran, 2001), rhesus monkeys (Hauser et al., 2000) and human infants (Feigenson et al., 2002), capuchin monkeys reliably chose the greater of two discrete quantities of food objects in our sequential presentation task. Even on their first test condition of one vs. two, participants chose the larger reward reliably above chance. Capuchins continued to perform above chance at other discriminations, performing reliably above chance when discriminating one vs. four and two vs. three, but not three vs. four.

In contrast to previous studies with infants (Feigenson et al., 2002) and rhesus macaques (Hauser et al., 2000), however, capuchins' performance in this experiment

seemed to depend not on the set-size of the

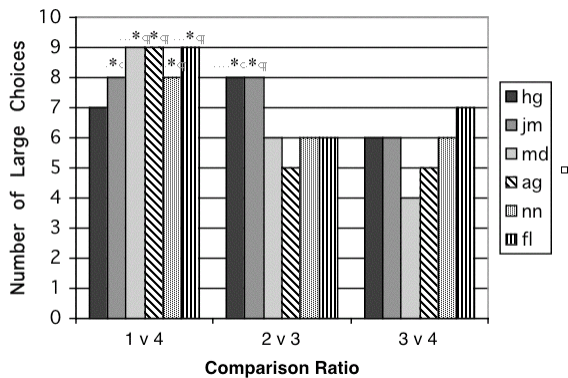


Figure 3. Number of trials (out of 10) in which individual monkeys chose the larger quantity of discrete food objects for each ratio condition in Experiment 1. Asterisks indicate that performance was significantly above chance (Binomial Test, $p < .05$).

two numerical comparisons, but instead on the ratio between the quantities presented. As the ratio between the two quantities approached 1:1, participants' performance decreased. Participants performed best on a one vs. four discrimination and worst on a three vs. four discrimination. Note that this pattern cannot be due to the overall number of items present in the display, as participants' performance on the one vs. four discrimination was reliably better than on the two vs. three discrimination, even though both of these comparisons involve five raisins in total.

Our results therefore contrast with those of human infants (Feigenson et al., 2002) and rhesus monkeys (Hauser et al., 2000) where performance was limited by the number of items in each bucket (the set size), rather than the ratio between the quantities. Our results are, however, consistent with recent research by Beran (2001, 2004) in which chimpanzees' tendency to choose the larger of two quantities of M&M's was found to be dependent on ratio, not set size, regardless of whether the number of objects in as set was inside or outside the object tracking

limit. This ratio signature suggests that analog magnitudes might underlie performance in this task. An account in which *only* object tracking was hypothesized, in contrast, would have predicted equivalent performance across the different comparisons until the set size limit was reached, at which point performance should have fallen to chance. The fact that our monkeys were only marginally above chance in the three vs. four comparison could be indicative of a set size limit of three in capuchins. However, the fact that they performed well above chance in the one vs. four comparison argues against this possibility. If capuchins were limited to representing only three items in each cup, then performance in three vs. four and one vs. four comparisons should have been equivalent. Nevertheless, the effect of ratio in the small number range is clear in this experiment and is inexplicable on an object tracking account. Thus, our data are consistent with the use of analog magnitudes to represent the quantities.

Given that capuchins apparently use analog magnitudes to quantify discrete objects, it is of interest to ask whether and how their quantification abilities extend to entities that cannot be enumerated using object indexes. Can capuchins enumerate *non-objects*, like substances? Previous research in both infants (Huntley-Fenner et al., 2002) and adults (vanMarle & Scholl, 2003) suggests that the object tracking mechanism is sensitive to the object status of entities to be tracked. That is, both infants and adults have relative difficulty tracking nonsolid substances compared to discrete objects. Our difficulty enumerating substances is evident in natural language; English, for example, employs different syntax and morphology for objects and substances, using count noun syntax for objects and mass noun syntax for substances.

As suggested by the term “count noun,” discrete objects can be counted, while substances cannot. Thus, it is appropriate to say “*three* bottles”, but not “*three* sands”. Conversely, while it is acceptable to say “*some* sand”, it is not acceptable to say “*some* bottle”. Children become sensitive to this distinction at a very early age, and subsequently use it to infer the appropriate referent of a count or mass noun (Soja, 1992; Soja, Carey, & Spelke, 1991; see also Hall, 1996; Prasada, 1999). Given the stark contrast between how humans appear to process objects and substances in these various domains, we wished to ask whether the same is true for other primate species.

The next experiment tested capuchins’ ability to choose the larger of two portions of a continuous substance--banana puree. For purposes of comparison to Experiment 1, we again ran an initial one vs. two comparison, followed by three further comparison conditions that were matched in ratio to the previous experiment--one vs. four, two vs. three, and three vs. four.

Experiment 2

Method

Participants. The same 6 monkeys from Experiment 1 were tested.

Materials. We conducted the experiment in the same enclosure as before, the only difference being that instead of yogurt raisins, the quantities consisted of amounts of banana puree. The puree was made immediately before each session by blending two ripe bananas with about 1/8 cup of water until it was a smooth, pourable consistency.

Design and Procedure. The design and procedure was identical to Experiment 1 with the following exceptions. Instead of placing raisins one by one into the cups, equal-sized scoops (one scoop was one-half of a miniature plastic egg, approximately 1.5” in diameter and 1” long) of banana puree were drawn one at a time from a small container and visibly poured into the cups from a height of about 5 cm. Each pouring event took approximately 2 seconds. As with

discrete quantities, there were no explicit controls for ‘duration of presentation’ or ‘rate of presentation’ and so they were generally confounded with overall amount. However, as before, they were less reliable cues than overall amount since there were again some trials in which the monkeys looked away during presentation causing the rate to vary and overall duration to increase for that quantity. Each scoop, for a given quantity, was poured directly on top of the last so that the final quantity consisted of a single portion. Once both quantities had been poured, the tray was immediately placed on the upper rails and the monkey was allowed to choose one of the quantities. As before, the experimenter avoided cuing the monkeys by looking directly ahead while lifting the tray. A choice was made when the monkey knocked one of the cups over and scooped up the banana puree. As before, the quantities were presented sequentially with side (left or right) and order (larger number placed first or second).

After completing an initial one vs. zero training phase, all monkeys began with the one vs. two Test condition, followed by the remaining Test Conditions (one vs. four, two vs. three, and three vs. four) in the same order they received them in the first experiment. Additional one vs. two Training sessions were presented between each test condition until the monkey got 80% correct in a single session. Training sessions were identical to the one vs. two test condition except the tray was pulled away if the monkey reached for the smaller quantity.

Results

All participants performed well above chance (Mean = 90%) across the first two sessions of their initial one vs. zero training phase. All 6 participants therefore moved onto the first one vs. two test. Participants performed above chance (58 +/- 8%) on this first test condition, choosing two poured banana scoops over one scoop ($t(5) = 2.71, p < 0.02$). However, despite that fact that participants were above chance on this one vs. two substance condition, their performance was reliably worse than that of the one vs. two object condition of Experiment 1 (58% vs. 75%; $t(5) = 2.99, p = 0.03$).

Participants then moved on to the additional comparisons. Average percent

correct was 77 +/- 12% (CI = 67-86%), 68 +/- 18% (CI = 54-83%), and 66 +/- 8% (CI = 59-72%) for one vs. four, two vs. three, and three vs. four, respectively (see Figure 2). Participants' performance was significantly above chance for all conditions (one vs. four, $t(5) = 5.39$, $p < 0.002$; two vs. three, $t(5) = 2.45$, $p < 0.03$; three vs. four, $t(5) = 4.91$, $p < 0.002$). A repeated measures ANOVA with condition (one vs. four, two vs. three, and three vs. four) as a within-subject factor revealed no significant effects. Although the trend did not quite reach significance ($F(2,10) = 2.01$, $p = .18$, $\eta^2_G = .10$), the average percent correct increased as the ratio between the quantities got larger. Non-parametric tests revealed the same ratio-dependent pattern of performance. We again used binomial tests to measure the reliability of each monkey's performance in each test condition (one vs. four, two vs. three, and three vs. four--see Figure 4). Results revealed that the number of monkeys reliably choosing the larger amount for the one vs. four, two vs. three, and three vs. four comparisons, respectively, was 3/6, 2/6, 1/6. An additional correlation analysis confirmed this pattern; as in Experiment 1, we again observed a highly significant negative correlation between ratio and performance ($r = -.57$, $t(34) = 4.04$, $p < 0.0003$). When the proportional similarity between the numbers increased, participants' performance decreased. Thus, as with discrete objects, monkeys' performance again appeared to be ratio-dependent; the larger the ratio between the substance quantities, the better the performance.

To explore performance across conditions and across Experiments 1 and 2, we performed a repeated-measures ANOVA with experiment (object and substance) and comparison (one vs. four, two vs. three, and three vs. four) as within subject factors. There was no main effect of experiment

($F(1,5) = 0.056$, $p = 0.82$, $\eta^2_G = 0.008$). Overall, participants performed similarly when faced with objects and substances. Our ANOVA did, however, reveal a significant effect of comparison ($F(2,10) = 7.83$, $p = 0.009$, $\eta^2_G = 0.48$). Across both studies, participants demonstrated a reliable pattern of performing best on the one vs. four comparison (81 +/- 12%; CI = 74-87%), slightly worse on the two vs. three comparison (67 +/- 15%; CI = 58-75%), and worst on the three vs. four comparison (61 +/- 10%; CI = 56-67%). As the ratio between the two items approached 1:1, participants' performance got worse. There was no interaction between experiment and condition ($F(2,10) = 2.36$, $p = 0.14$); participants demonstrated the same pattern of performance across both Experiments 1 and 2.

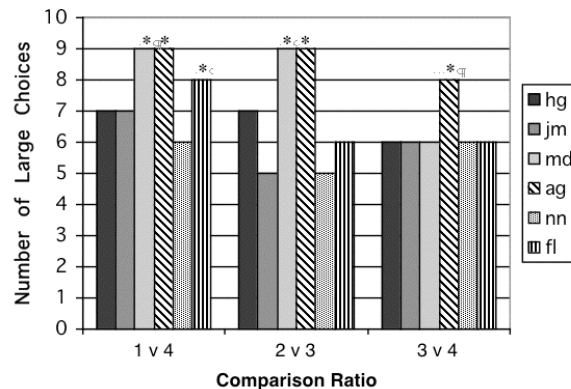


Figure 4. Number of trials (out of 10) in which individual monkeys chose the larger quantity of substance for each ratio condition in Experiment 2. Asterisks indicate that performance was significantly above chance (Binomial Test, $p < .05$).

Discussion

Capuchins are able to quantify and compare different amounts of a continuous substance just as well as they quantify the same amounts (i.e., ratios) of discrete objects. Capuchins selected the larger of the two

quantities significantly more often than chance across all ratio comparisons. As in the first experiment, performance was ratio-dependent--the bigger the proportional difference, the more likely participants were to select the larger amount. Monkeys, like human infants (vanMarle, 2004), can represent quantities of a nonsolid substance, compute the total amount of substance in each quantity, and compare these representations. One potential concern with this interpretation is that the total amount of substance in each quantity was perfectly confounded with the 'number of pouring events'. Thus, monkeys could have selected the larger quantity by counting the 'number of pouring events' instead of computing the total amount of substance in each quantity. Although a valid concern, the fact that performance was reliably above chance in the three vs. four Substance condition, but not the three vs. four Object condition, argues against this possibility. If they had been counting the number of hiding events, then one would expect them to show equivalent performance in both cases.

General Discussion

The experiments reported here examined capuchin monkeys' ability to quantify objects and substances. Consistent with previous results with nonhuman primates (Beran, 2001; Hauser et al., 2000) and human infants (Feigenson et al., 2002; vanMarle, 2004), capuchin monkeys are able to quantify discrete quantities of food and when given a choice between two quantities, they reliably choose the larger amount. The present study extended these earlier results by comparing capuchin monkeys' ability to quantify discrete objects versus continuous substances. Previous work with infants (Huntley-Fenner et al., 2002; vanMarle, 2004) and adults

(vanMarle & Scholl, 2003) suggests that tracking substances is more difficult than tracking discrete objects. The present findings are somewhat in accord with these previous findings; on their first one vs. two test session, monkeys performed reliably better at discriminating objects than substances. That said, unlike infants and adults, our capuchins performed above chance at both object *and* substance discriminations. In this sense, our findings are also consistent with recent research comparing infants' ability to quantify substances and objects in a similar object choice task (vanMarle, 2004). In that study, 10- and 12- month-old infants were able to represent and compare the magnitudes of two hidden portions of food substance, but their ability to do so was limited compared to their discrete quantification abilities. Thus, although processing substances appears to be somewhat more difficult than processing discrete objects, both human and nonhuman primates may have some way of representing *amount of "stuff"* in addition to *discrete numbers of objects*. Of course, given that 'amount of stuff' was confounded with other discrete cues (e.g., 'number of pours') in Experiment 2, our results with capuchins should be viewed with caution. We predict however, that capuchins would still show successful (and ratio-dependent) performance if tested under conditions that ruled out discrete cues to "amount of stuff".

One obvious question to ask is whether the same mechanisms thought to underlie discrete quantification (an analog magnitude mechanism and an object tracking system) also underlie monkeys' ability to quantify continuous substances. Our present results support the view that monkeys may be using analog magnitudes in both cases. First, monkeys were successful at discriminating the two quantities regardless of whether the food quantities were sets of discrete

individuals or substances. Second, capuchins' performance was dependent on the ratio between the two numbers to be discriminated; such ratio-based performance is a classic signature of an analog magnitude mechanism.

For these reasons, our results suggest that nonhuman primates can use analog magnitudes to represent small sets of discrete objects. Moreover, given that the object tracking system is both sensitive to whether an entity is an object or a portion of substance, and has difficulty tracking entities that move like nonsolid substances (i.e., extend/contract, disintegrate, etc.), it seems unlikely that the capuchins were using this mechanism to quantify the substances in Experiment 2. Therefore, the similarity in performance across Experiments 1 and 2 is more consistent with the notion that the capuchins were using analog magnitudes to represent the quantities in both cases.

Our results add to an increasingly puzzling picture about which types of mechanisms underlie nonverbal quantity representations in different tasks. On one hand, both preverbal infants (Feigenson et al., 2002) and rhesus monkeys (Hauser et al., 2000) show clear set size limitations in an ordinal choice task, consistent with an object tracking account. In contrast, chimpanzees (Beran, 2001, 2004), orangutans (Call, 2000), and now capuchins show clear ratio-dependent performance, consistent with an analog magnitude account (see also Lewis et al., 2005, for a similar findings in a slightly different task with lemurs). Is there a way to rectify these sets of findings? One possibility concerns the way in which the two sets of studies were conducted. Both Feigenson et al. (2002) and Hauser et al. (2000) collected only a single data point for each participant. Such between-subject analyses make it difficult to observe possibly subtle differences in performance across different ratio

comparisons. Previous research with chimpanzees (Beran, 2001, 2004), in addition to the present studies, used a more sensitive paradigm by testing individual participants on multiple trials and multiple comparisons. In both cases, this approach revealed differences in performance that were dependent on ratio. It is possible, then, that rhesus monkeys (and possibly human infants) would show ratio-dependent performance if tested on multiple trials of the same numerical comparison in an ordinal choice task. A second possibility concerns the role of multiple trials in determining which nonverbal number system begins to operate. It is possible that seeing multiple numerical comparisons together somehow engages the analog magnitude system in a way that single presentations would not. This alternative makes the prediction that capuchin monkeys tested with single trials would perform much like infants and rhesus monkeys, demonstrating a set-size limit rather than ratio-dependent performance.

Since these experiments represent an initial attempt to observe successful quantity-based responding in a primate species whose quantitative abilities have been relatively neglected (but see Judge et al., 2005), they face some limitations. First, in order to find strong evidence that capuchins are really using analog magnitudes rather than object indexes to quantify objects and substances, it is necessary to test quantities that exceed the supposed set size limit but are of a discriminable ratio. For example, based on the present results, if capuchins are using analog magnitudes in our task, then they should be able to reliably choose the larger quantity when presented comparisons of three vs. six raisins. In fact, we attempted to test this exact comparison, but due to methodological difficulties, the results were not interpretable. Specifically, we found that: (a) the monkeys became satiated quickly (from obtaining such

a large number of raisins), which resulted in lowered motivation and failure to complete a full testing session, and (b) the amount of time necessary to hide six raisins apparently exceeded our monkeys' attention span which resulted in their being increasingly more likely to stop participating as the session went on. Future studies will attempt to obtain this critical data by having monkeys complete shorter sessions across separate testing days.

Second, further research is necessary to rule out temporal cues to amount that covaried with the dimensions of interest (number for Experiment 1, amount for Experiment 2). In particular, future studies will profit from controlling the 'rate of presentation', 'duration of presentation', and 'number of pouring events'. Doing so will allow for the further investigation of the conditions under which object indexes or analog magnitudes are employed in the absence of these cues. It should be noted however, that analog magnitudes are not specific to number representation. In fact, they were originally used to account for rats' ability to represent temporal intervals (Scalar Expectancy Theory; Gibbon, 1977) and later proposed to underlie rats' ability to represent number (Meck & Church, 1983). Thus, even if our capuchins were responding on the basis of temporal attributes of the presentation sequences (which we feel is unlikely for the reasons discussed in the methods sections), this is still consistent with the conclusion that performance was based on the use of analog magnitudes. In addition, if this were the case, it would further rule out the possibility that they were using object indexes since object tracking models have no provision whatsoever for the representation of temporal properties of events or event sequences.

In conclusion, the present data contribute to the ongoing debate regarding the nature of the representations that underlie

nonverbal ordinal judgments for discrete quantities. Our capuchin findings also go a step further by examining whether performance differs depending on whether the quantified entities are discrete objects or continuous substances. The results support the notion that capuchin monkeys may use analog magnitudes to quantify small sets of discrete objects and portions of continuous substances. Further research is necessary to elucidate the precision with which capuchins can quantify objects and substances and the conditions under which an organism will use either analog magnitudes or object indexes to represent a given quantity. Answers to these questions will inform not only theories of comparative cognition and cognitive development, but will also contribute to the broader question of how organisms represent quantitative information in their environment and use it to guide their behavior.

References

- Beran, M. J. (2001). Summation and numerosness judgments of sequentially presented sets of items by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *115*, 181-191.
- Beran, M. J. (2004). Chimpanzees (*Pan troglodytes*) respond to nonvisible sets after one-by-one addition and removal of items. *Journal of Comparative Psychology*, *118*, 25-36.
- Beran, M. J., & Beran, M. M. (2004). Chimpanzees remember the results of one-by-one addition of food items to sets. *Psychological Science*, *15*, 94-99.
- Beran, M. J., & Rumbaugh, D. M. (2001). "Constructive" enumeration by chimpanzees (*Pan troglodytes*) on a computerized task. *Animal Cognition*, *4*, 81-89.

- Boysen, S. T., & Berntson, G. G. (1989). Numerical competence in a chimpanzee (*Pan troglodytes*). *Journal of Comparative Psychology*, *103*, 23-31.
- Brannon, E. M., & Roitman, J. (2003). Nonverbal representations of time and number in nonhuman animals and human infants. In W. Meck (Ed.), *Functional and Neural Mechanisms of Interval Timing* (pp. 143-182). New York: CRC Press.
- Brannon, E. M. & Terrace, H. S. (1998). Ordering of the numerosities 1-9 by monkeys. *Science*, *282*, 746-749.
- Brannon, E. M. & Terrace, H. S. (2000). Representation of the numerosities 1-9 by rhesus macaques (*Macaca mulatta*). *Journal of Experimental Psychology: Animal Behavior Processes*, *26*, 31-49.
- Brannon, E. M., Wusthoff, C. J., Gallistel, C. R., & Gibbon, J. (2001). Numerical subtraction in the Pigeon: Evidence for a linear subjective number scale. *Psychological Science*, *12*(3), 238-243.
- Call, J. (2000). Estimating and operating on discrete quantities in Orangutans (*Pongo pygmaeus*). *Journal of Comparative Psychology*, *114*(2), 136-147.
- Cordes, S., Gelman, R., Gallistel, C. R. & Whalen, J. (2001). Variability signatures distinguish verbal from nonverbal counting for both large and small numbers. *Psychological Bulletin and Review*, *8*, 698-707.
- Davis, H., & Perusse, R. (1988). Numerical competence in animals: Definitional issues, current evidence, and a new research agenda. *Behavioral and Brain Sciences*, *11*(4), 561-615.
- Dehaene, S. & Changeaux, J. P. (1993). Development of elementary numerical abilities: A neural model. *Journal of Cognitive Neuroscience*, *5*, 390-407.
- Dehaene, S. (1997). *The number sense*. Oxford: Oxford University Press.
- Feigenson, L. & Carey, S. (2003). Tracking individuals via object-files: Evidence from infants' manual search. *Developmental Science*, *6*, 568-584.
- Feigenson, L., Carey, S., & Hauser, M. D. (2002). The representations underlying infants' choice of more: object files versus analog magnitudes. *Psychological Science*, *13*, 150-156.
- Feigenson, L., Dehaene, S., & Spelke, E.S. (2004). Core systems of number. *Trends in Cognitive Sciences*, *8*(7), 307-314.
- Fernandes, D. M. & Church, R. M. (1982). Discrimination of the number of sequential events by rats. *Animal Learning & Behavior*, *10*, 171-176.
- Flombaum, J. I., Junge, J. A., & Hauser, M. D. (2005). Rhesus monkeys (*Macaca mulatta*) spontaneously compute addition operations over large numbers. *Cognition*, *97*, 315-325.
- Fragaszy, D. M., Visalberghi, E., & Fedigan, L. M. (2004). *The Complete Capuchin: The Biology of the Genus Cebus*. New York: Cambridge University Press.
- Gallistel, C. R. & Gelman, R. (2000). Nonverbal numerical cognition: From reals to integers. *Trends in Cognitive Sciences*, *4*, 59-65.
- Gallistel, C. R. & Gelman, R. (2005). Mathematical Cognition. In K. Holyoak & R. Morrison (Eds.) *The Cambridge handbook of thinking and reasoning* (pp. 559-588). New York: Cambridge University Press.
- Gibbon, J. (1977). Scaler expectancy theory and Weber's law in animal timing. *Psychological Review*, *84*, 279-325.
- Hall, G. (1996). Naming solids and nonsolids: Children's default construals. *Cognitive Development*, *11*, 229-264.

- Hauser, M. D., & Carey, S. (2003). Spontaneous representations of small numbers of objects by rhesus macaques: Examination of content and format. *Cognitive Psychology*, *47*(4), 367-401.
- Hauser, M. D., Carey, S., & Hauser, L. B. (2000). Spontaneous number representation in semi-free-ranging rhesus monkeys. *Proceedings of the Royal Society, London*, *267*, 829-833.
- Hauser, M. D., MacNeilage, P., & Ware, M. (1996). Numerical representations in primates. *Proceedings of the National Academy of Sciences*, *93*, 1514-1517.
- Hauser, M. D. & Spelke, E. (2004). The evolutionary and developmental foundations of human knowledge: A case study of mathematics. In M. Gazzaniga (Ed.) *The Cognitive Neurosciences III* (pp. 853-864). Cambridge: MIT Press.
- Hauser, M. D., Tsao, F., Garcia, P., & Spelke, E. S. (2003). Evolutionary foundations of number: spontaneous representation of numerical magnitudes by cotton-top tamarins. *Proceedings of the Royal Society, London, Series B*, *270*, 1441-1446.
- Howell, D. C. (1997). *Statistical Methods for Psychology*. (4th ed.). Belmont, CA: Wadsworth Publishing Company.
- Huntley-Fenner, G. (1995). The representation of objects, non-solid substances, and collections in infancy and early childhood. (Doctoral dissertation, Massachusetts Institute of Technology [MIT], 1995). *Dissertation Abstracts International: Section B: The Sciences & Engineering*, *56*(4-B), 2352.
- Huntley-Fenner, G., Carey, S., & Solimando, A. (2002). Objects are individuals but stuff doesn't count: Perceived rigidity and cohesiveness influence infants' representations of small numbers of discrete entities. *Cognition*, *85*, 203-221.
- Jordan, K. E., Brannon, E. M., Logothetis, N. K. & Ghazanfar, A.A. (2005) Monkeys match the number voices they hear to the number of faces they see. *Current Biology*, *15*, 1034-1038.
- Judge, P. G., Evans, T. A., & Vyas, D. K. (2005). Ordinal representation of numeric quantities by brown capuchin monkeys (*Cebus apella*). *Journal of Experimental Psychology: Animal Behavior Processes*, *31*, 79-94.
- Kahneman, D., Treisman, A., & Gibbs, B.J. (1992). The reviewing of object files: Object-specific integration of information. *Cognitive Psychology*, *24*, 174-219.
- Lewis, K. P., Jaffe, S., & Brannon, E. M. (2005). Analog number representations in mongoose lemurs (*Eulemur mongoz*): Evidence from a search task. *Animal Cognition*, *8*(4), 247-252.
- McCrink, K., & Wynn, K. (2004). Large-number addition and subtraction in infants. *Psychological Science*, *15*, 776-781.
- Mechner, F. (1958). Probability relations within response sequences under ratio reinforcement. *Journal of the Experimental Analysis of Behavior*, *1*, 109-122.
- Meck, W. H., & Church, R. M. (1983). A mode control model of counting and timing processes. *Journal of Psychological Animal Behavior Processes*, *9*(3), 320-34.
- Nieder, A. (2005). Counting on Neurons: The Neurobiology of Numerical Competence. *Nature Reviews Neuroscience*, *6*(3), 177-190.
- Nieder, A., Freedman, D. J., & Miller, E.K. (2002). Representation of the Quantity of Visual Items in the Primate

- Prefrontal Cortex. *Science*, 297, 1708-1711.
- Nieder, A. & Miller, E.K. (2003). Coding of Cognitive Magnitude: Compressed Scaling of Numerical Information in the Primate Prefrontal Cortex. *Neuron*, 37, 149-157.
- Nieder, A. & Miller, E.K. (2004). Analog Numerical Representations in Rhesus Monkeys: Evidence for Parallel Processing. *Journal of Cognitive Neuroscience*, 16, 889-901.
- Olejnik, S. & Algina, J. (2003). Generalized Eta and Omega Squared Statistics: Measures of Effect Size for Some Common Research Designs. *Psychological Methods*, 8(4), 434-447.
- Prasada, S. (1999). Names of things and stuff: An Aristotelian perspective. In R. Jackendoff, P. Bloom, & K. Wynn (Eds.), *Language, logic, and concepts: Essays in memory of John Macnamara* (pp. 119-146). Cambridge, MA: MIT Press.
- Pylyshyn, Z. W. (1989). The role of location indexes in spatial perception: A sketch of the FINST spatial-index model. *Cognition*, 32, 65-97.
- Pylyshyn, Z. W., & Storm, R. W. (1988). Tracking Multiple Independent Targets: Evidence for a Parallel Tracking Mechanism. *Spatial Vision*, 3(3), 179-197.
- Santos, L. R., Barnes, J. L. & Mahajan, N. (2005). Expectations about numerical events in four lemur species (*Eulemur fulvus*, *Eulemur mongoz*, *Lemur catta* and *Varecia rubra*). *Animal Cognition*, 8(4), 253-262.
- Scholl, B. J., Pylyshyn, Z. W., & Feldman, J. (2001). What is a visual object? Evidence from target merging in multiple object tracking. *Cognition*, 80, 159-177.
- Simon, T. J. (1997). Reconceptualizing the origins of number knowledge: A “non-numerical” account. *Cognitive Development*, 12, 349-372.
- Soja, N.N. (1992). Inferences about the meanings of nouns: The relationship between Perception and syntax. *Cognitive Development*, 7, 29-45.
- Soja, N.N., Carey, S., & Spelke, E.S. (1991). Ontological categories guide young children’s inductions of word meaning: Object terms and substance terms. *Cognition*, 38, 179-211.
- vanMarle, K. L. (2004). Infants' understanding of number: The relationship between discrete and continuous quantity. (Doctoral dissertation, Yale University, 2004). *Dissertation Abstracts International: Section B: The Sciences & Engineering*, 65(3-B), 1582. US: Univ Microfilms International.
- vanMarle, K., & Scholl, B. J. (2003). Attentive Tracking of Objects Versus Substances. *Psychological Science*, 14(5), 498-504.
- Whalen, J., Gallistel, C. R., & Gelman, R. (1999). Nonverbal counting in humans: the psychophysics of number representation. *Psychological Science*, 10, 130-137.
- Wynn, K. (1992). Addition and subtraction by human infants. *Nature*, 358, 749-750.
- Xu, F. (2003). Numerosity discrimination in infants: Evidence for two systems of representations. *Cognition*, 89, B15-B25.
- Xu, F., & Spelke, E. S. (2000). Large number discrimination in 6-month old infants. *Cognition*, 74, B1-B11.
- Xu, F., Spelke, E. S., & Goddard, S. (2005). Number sense in human infants. *Developmental Science*, 8(1), 88-101.