

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? Results of previous research with human infants suggest 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 finding suggests that capuchins quantify objects and substances similarly and do so via analog magnitude representations.

Keywords: discrete quantity, continuous quantity, analog magnitudes, nonhuman primates, nonsolid substances

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 nonlinguistic 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, Evans, & Vyas, 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, and 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 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 in 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 on their absolute

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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 because 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 they respond to the numerosity of sequentially presented stimuli. Meck and Church's (1983) accumulator model, however, can explain how numerosity might be represented for both simultaneous and sequentially presented stimuli.

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

It is interesting that human infants and various animals seem to abstract the number 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.

In 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. Detecting a mismatch between the number of indexes and the number of visible items is thought to account for the fact that infants, monkeys, and lemurs look longer at numerically incorrect than at numerically correct outcomes in such situations (Hauser et al., 1996; Santos, Barnes, & Mahajan, 2005; Simon, 1997; Wynn, 1992).

Previously, researchers studying both infants and nonhuman primates have examined which of these two types of mechanisms—analogue magnitude representations or object tracking mechanisms—underlies nonverbal number processing. Much of this work has been designed to rule out one mechanism or the other as an explanation for animals’ ability to respond on the basis of numbers. Recently however, a growing body of evidence has begun to support the idea that human and nonhuman animals may use 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, findings that in turn would provide information about the nature and limits of each of the two mechanisms.

One recent proposal is that analogue 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 analogue magnitudes represent only large values (i.e., more than four). Limited evidence for this comes from studies of infants’ numerical processing.² For example, human infants fail to discriminate small values at a 1:2 ratio (e.g., 1 dot vs. 2 dots: Xu, 2003), even though they readily discriminate larger values at a 1:2 ratio (e.g., 8 dots 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., two crackers over one,³ three crackers over two; see Feigenson et al., 2002). Performance fell to chance, however, whenever there were more than three crackers hidden in a given container (e.g., three vs. four, one vs. four). 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 analogue magnitudes were being used (i.e., one cracker vs. four 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 three objects (Feigenson & Carey, 2003; Feigenson et al., 2002).

A second proposal concerning differences in the use of analogue magnitudes and object indexes involves the nature of the units over which these two types of mechanisms operate. Previous results from investigations of object tracking processes in adults suggest that this system might be limited to tracking rigid, cohesive objects (vanMarle & Scholl, 2003). In a standard multiple object tracking task (Pylyshyn & Storm, 1988), adults were asked to track four of eight 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 performed near

² Note, however, that evidence from human adults (Cordes et al., 2001) shows that the accumulator represents both large and small values. When adults were 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).

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 numbers. Under these conditions, infants successfully discriminate between small values as long as the number of items in a set does not exceed three.

chance when the items were noncohesive substances that “poured” from location to location. Taken together with studies showing that adults have difficulty tracking other nonobject entities (e.g., parts, Scholl, Pylyshyn, & Feldman, 2001), this finding 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 reliably looked longer when 1 object + 1 object were shown to equal only 1 object (a physically impossible and 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.

Note, however, that infants can quantify substances under some circumstances. For example, 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 a 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 material (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 noncohesiveness was made salient. Results indicated that in the object condition, infants readily selected two crackers over one (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 vs. 20 Cheerios) performed at chance. In contrast, those given a choice between quantities differing by a 1:4 ratio (5 vs. 20 Cheerios) reliably chose the larger amount. Because the food in this case violated cohesion (a property known to disrupt visual tracking in human adults) and because 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, with which they succeeded at a 1:4 ratio but not at 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 of objects and substances. But what about nonhuman animals? Although 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 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 1–7). The chimps performed above chance with all values, and their performance was consistent with analog representations of numbers: The larger the quantity to be matched, the worse the chimps performed (Beran & Rumbaugh, 2001). Further evidence for analog magnitudes was obtained using a different task in which chimpanzees saw different numbers of M&Ms sequentially placed into two cups. Here, chimpanzees chose the cup with greater number of candies significantly more often than could be attributed to chance, even when the cup 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 findings, 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. The monkeys reliably chose the box containing the larger number of food items for a variety of comparisons including one versus two, two versus three, and three versus four but chose randomly when offered four versus

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

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.

six, three versus eight, and four versus eight. Hauser and colleagues argued that this set-size limit showed that rhesus monkeys were using object indexes, rather than analog magnitudes, 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 versus eight and three versus eight, suggesting that the monkeys, like the infants, generally failed to use analog magnitudes 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, because of the design of these studies, they do not provide information about what discrimination function obtains in this task; each monkey was tested only once, so there is no way to see if the rhesus monkey participants showed subtle differences in performance that depended on the ratio comparison. Moreover, because different animals participated in different conditions, meaningful comparisons cannot be made across conditions. In the present study, we aimed 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 that, 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 those used by 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 this species could choose the greater of two hidden quantities of food in an ordinal choice task. Experiment 2 was designed to explore whether capuchins could quantify nonobject 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; participants were born in captivity either at that facility or at the Living Links Center capuchin colony in Yerkes Regional Primate Research Center in Atlanta, GA. Our participant group consisted of 3 males and 3 females ranging in age from 3 years 4 months to 9 years 1 month, with a mean age of 6 years 5 months 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 received 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 hidden 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 the monkey entered the experimental enclosure, a Plexiglas door was closed behind it. 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 × 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 × 61 cm) with two sets of rails. These rails supported an acrylic tray (58.5 cm long × 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 the quantities would be accessible through the hand holes in the panel, we secured two white plastic plates (15.25 cm in diameter) on the front half of the tray to serve as place markers. The plates were covered with gray duct tape so the food items placed on them would be visible. This step also minimized any potential auditory cues made by the sound of the food items dropping onto the plates.⁶ To facilitate comparison to subsequent experiments, we used two red plastic cups (~4 in. [10.16 cm] tall and 3 in. [7.62 cm] in diameter at the opening) to cover food items by placing them upside-down over the quantities. The monkeys could not see the food items once hidden.

We used yogurt raisins,⁷ a highly preferred food with which the participants had prior experience. Because 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 as a cue for two additional reasons. First, our food items had a yogurt coating that softened within 2–3 min of being brought into the testing area because of the high heat and humidity, so that they made little sound when landing on the plates. Additionally, because 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 and noise generated by monkeys leaping from swing to swing and climbing around the enclosure) 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 United States.

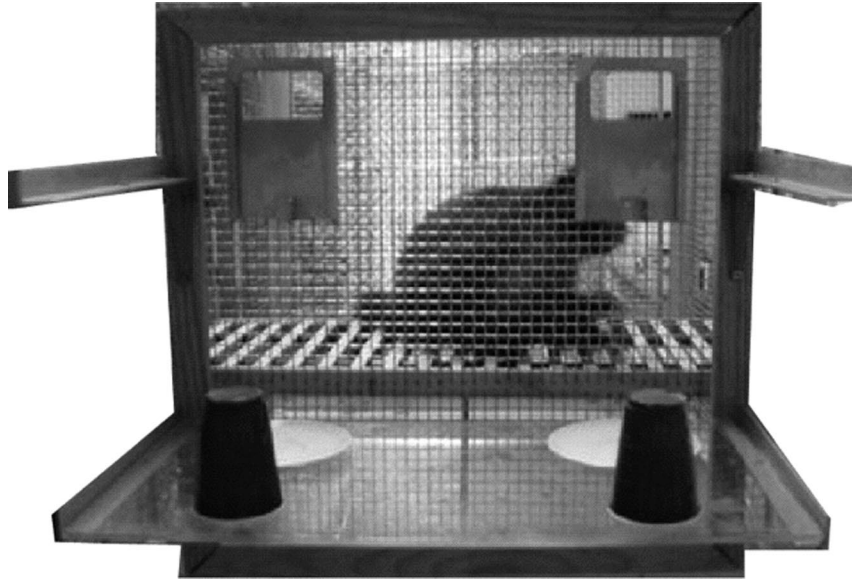


Figure 1. An experimenter's eye view of the testing chamber setup. The Plexiglas tray with two plastic plates serving as place markers was presented on the wood frame. The two red plastic cups were movable and used to hide food items during presentations.

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 the monkey 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 participant's name. To ensure that the monkeys saw each placement, the experimenter did not place a yogurt raisin into the cup unless the monkey was attending to the event. Because 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 side order (left first or right first) counterbalanced across trials. Once all the raisins had been dropped into the cups, the experimenter tapped the center of the tray frame until the monkey centered itself between the two hand holes. Then 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 versus two test session consisting of 10 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 versus two test session, they went on to additional testing sessions, each of which involved one of the three other numerical comparisons of interest—either one versus four, two versus three, and three versus 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 versus 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 conducted interim training sessions for the participants 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 versus 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, which allowed them to continue onto the initial one versus two test session. Participants performed above chance ($M \pm SD = 75\% \pm 14\%$) on this initial test condition; on average, all 6 monkeys chose two raisins over one raisin, $t(5) = 4.44$, $p < .003$.

Participants then moved onto the additional test conditions. Mean $\pm SD$ percentage correct was $85\% \pm 10\%$ (confidence interval [CI]⁸ = 77%–93%) for one versus four, $65\% \pm 12\%$ (CI = 55%–75%) for two versus three, and $57\% \pm 10\%$ (CI = 48%–65%) for three versus four (see Figure 2). We used t tests to compare performance on each comparison against chance performance (50%). Performance was significantly better than chance in the one versus four condition, $t(5) = 8.17$, $p = .0002$, and the two versus three condition, $t(5) = 3.00$, $p = .02$, but was only marginally above chance in the three versus four condition, $t(5) = 1.58$, $p = .09$. We then performed a repeated measures analysis of variance (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, $F(2, 10) = 8.01$, $p = .008$, $\eta_G^2 = 0.43$.⁹ Participants performed significantly differently across the three test comparisons, with highest performance on the discriminations involving the largest 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, we performed a correlation between the ratio

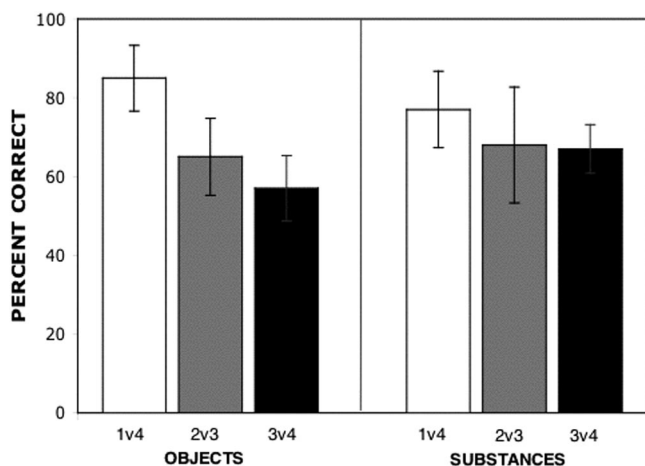


Figure 2. Mean percentage of correct responses (including 95% confidence intervals) across different numerical comparisons in object (Experiment 1) and substance (Experiment 2) conditions.

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 $r = -0.75$, $t(16) = 4.60$, $p < .0003$; as the proportional similarity between the numbers increased, participants' performance decreased.

Nonparametric tests revealed a similar pattern. We used a binomial test 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 3). Results revealed that the number of monkeys reliably choosing the larger amount was 5 of 6 for the one versus four, 2 of 6 for the two versus three, and 0 of 6 for the three versus four comparisons, respectively. Thus, despite substantial individual differences, the monkeys' performance again appeared to be ratio dependent. The larger the proportional difference between the amounts, the more the monkeys' performance improved.

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 versus 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 versus four and two versus three but not three versus 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 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 versus four discrimination and worst on a three versus four discrimination. Note that this pattern cannot be due to the overall number of items present in the display because participants' performance on the one versus four discrimination was reliably better than on the two versus three discrimination, even though both of these comparisons involved a total of five raisins.

Our results therefore contrast with those of studies of human infants (Feigenson et al., 2002) and rhesus monkeys (Hauser et al.,

⁸ All CIs reported in this article were computed with 95% confidence limits.

⁹ As a measure of effect size, we used η_G^2 (generalized eta squared). To have a sense of how this measure should be interpreted, the reader should consider it to be 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 $\eta_G^2 = .43$, 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 because it would prevent one from comparing effect sizes across similar studies using different designs.

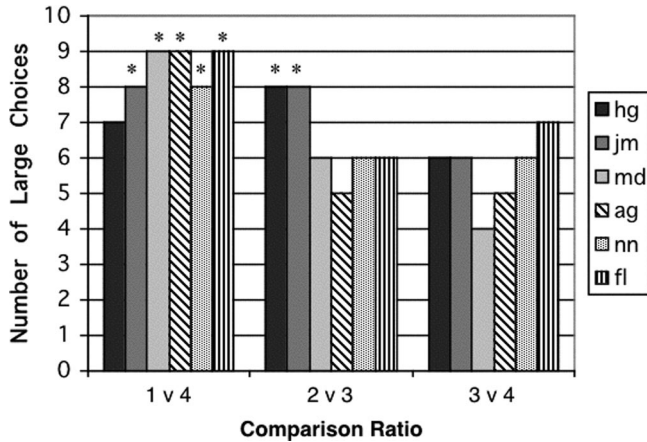


Figure 3. Number of trials (of 10) in which individual monkeys—3 females (hg, jm, md) and 3 males (ag, nn, fl)—chose the larger quantity of discrete food objects for each ratio condition in Experiment 1. Asterisks indicate that performance was significantly above chance (binomial test, $p < .05$).

2000) in which performance was limited by the number of items in each bucket (the set size), rather than by 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&Ms was found to be dependent on ratio, not set size, regardless of whether the number of objects in a set was inside or outside the object tracking limit. This ratio signature suggests that analog magnitudes might underlie performance in this task. In contrast, in an account in which only object tracking was hypothesized, the prediction would have been of 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 performed only marginally above chance in the three versus 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 versus four comparison argues against this possibility. If capuchins were limited to representing only three items in each cup, then performance in three versus four and one versus four comparisons should have been equivalent. Nevertheless, the effect of ratio in the small number range is clear in this experiment and is inexplicable with 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 nonobjects such as substances? Previous research results in both infants (Huntley-Fenner et al., 2002) and adults (vanMarle & Scholl, 2003) suggest 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 with tracking discrete objects. Our difficulty enumerating substances is evident in natural language; English, for example, uses 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, whereas substances cannot. Thus, it is appropriate to say “three bottles” but not “three sands.” Conversely, although 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 with Experiment 1, we again ran an initial one versus two comparison, followed by three further comparison conditions that were matched in ratio to the previous experiment—one versus four, two versus three, and three versus 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 (29.57 cc) of water until the mixture had a smooth, pourable consistency.

Design and procedure. The design and procedure were identical to those used in 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. [3.81 cm] wide and 1 in. [2.54] long) of banana puree were drawn one at a time from a small container and visibly poured through the holes in the cups from a height of approximately 5 cm. Each pouring event took approximately 2 s. As with discrete quantities, there were no explicit controls for duration of presentation or rate of presentation, and so they were generally confounded with the overall amount. However, as before, they were less reliable cues than overall amount because 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. 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 monkey 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) counterbalanced.

After completing an initial one versus zero training phase, all monkeys began with the one versus two test condition, followed by the remaining test conditions (one versus four, two versus three, and three versus four) in the same order they had received them in the first experiment. Additional one versus 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 versus two test condition except the tray was pulled away if the monkey reached for the smaller quantity.

Results

All participants performed well above chance ($M = 90%$) across the first two sessions of their initial one versus zero training phase.

All 6 participants therefore moved onto the first one versus two test. Participants performed above chance ($58\% \pm 8\%$) on this first test condition, choosing two poured banana scoops over one scoop, $t(5) = 2.71, p < .02$. However, despite the fact that participants were above chance on this one versus two substance condition, their performance was reliably worse than that in the one versus two object condition of Experiment 1 (58% vs. 75%); $t(5) = 2.99, p = .03$.

Participants then went on to the additional comparisons. Average percentage correct was $77\% \pm 12\%$ (CI = 67% – 86%) for one versus four, $68\% \pm 18\%$ (CI = 54% – 83%) for two versus three, and $66\% \pm 8\%$ (CI = 59% – 72%) for three versus four (see Figure 2). Participants' performance was significantly above chance for all conditions: one versus four, $t(5) = 5.39, p < .002$; two versus three, $t(5) = 2.45, p < .03$; and three versus four, $t(5) = 4.91, p < .002$. 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, $F(2, 10) = 2.01, p = .18, \eta_G^2 = .10$, the average percentage correct increased as the ratio between the quantities got larger. Nonparametric 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 versus four comparison was 3 of 6, for the two versus three comparison was 2 of 6, and for the three versus four comparison was 1 of 6. An additional correlation analysis confirmed this pattern; as in Experiment 1, we again observed a highly significant negative correlation between ratio and performance, $r = -.57, t(34) = 4.04, p < .0003$. 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, $F(1, 5) = 0.056, p = .82, \eta_G^2 = 0.008$. Overall, participants performed similarly when faced with objects and substances. Our ANOVA did, however, reveal a significant effect of comparison, $F(2, 10) = 7.83, p = .009, \eta_G^2 = 0.48$. Across both studies, participants showed a reliable pattern of performing best on the one versus four comparison ($81\% \pm 12\%$; CI = 74% – 87%), slightly worse on the two vs. three comparison ($67\% \pm 15\%$; CI = 58% – 75%), and worst on the three vs. four comparison ($61\% \pm 10\%$; CI = 56% – 67%). As the ratio between the two items approached 1:1, participants' performance declined. There was no Experiment \times Condition interaction, $F(2, 10) = 2.36, p = .14$; participants showed the same pattern of performance across both Experiments 1 and 2.

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 substance 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 that is a valid concern, the fact that performance was reliably above chance in the three versus four substance condition but not in the three versus four objects condition makes this possibility unlikely. If the monkeys 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 in this article were performed to examine 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 results of the present study extended these earlier results by comparing capuchin monkeys' ability to quantify discrete objects with their ability to quantify 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 versus two test session, monkeys performed reliably better at discriminating objects than at discriminating substances. That said, unlike infants and adults, our capuchins performed above chance at both object and substance discriminations. In this

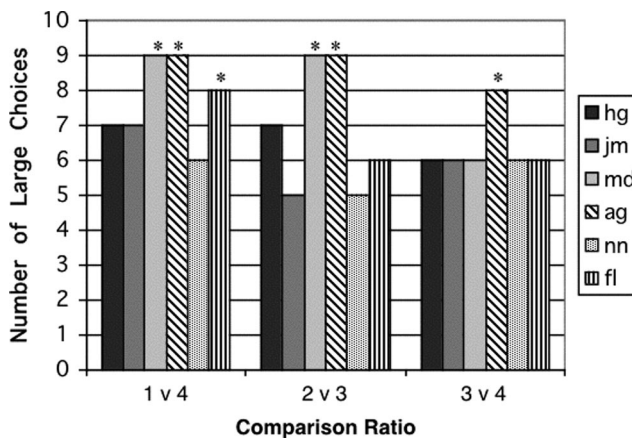


Figure 4. Number of trials (of 10) in which individual monkeys—3 females (hg, jm, md) and 3 males (ag, nn, fl)—chose the larger quantity of substance for each ratio condition in Experiment 2. Asterisks indicate that performance was significantly above chance (binomial test, $p < .05$).

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 with 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 the 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 have shown 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, the 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 (e.g., extend, contract, disintegrate), 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 the 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. On the other hand, 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 similar findings in a slightly different task with lemurs). Is there a way to reconcile 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 do not. This alternative leads one to the prediction that capuchin monkeys tested with single trials would perform much like infants and rhesus monkeys, showing a set-size limit rather than ratio-dependent performance.

Because 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), there are some limitations. First, strong evidence that capuchins are really using analog magnitudes rather than object indexes to quantify objects and substances requires testing of quantities that exceed the supposed set size limit but are of a discriminable ratio. For example, on the basis of 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 with comparisons of three versus six raisins. In fact, we attempted to test this exact comparison but because of 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 likely to stop participating as the session went on. In future studies, we 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 would profit from controlling the rate of presentation, duration of presentation, and number of pouring events. Doing so would allow the further investigation of the conditions under which object indexes or analog magnitudes are used 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 numbers (Meck & Church, 1983). Thus, even if our capuchins were responding on the basis of temporal attributes of the presentation sequences (which we believe is unlikely for the reasons discussed in the Method 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 because 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 findings in capuchins also go a step further by examining whether performance when the quantified entities are discrete objects differs from performance when the quantified entities are 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 uses either analog magnitudes or object indexes to represent a given quantity. Answers to these questions not only will inform theories of comparative cognition and cognitive development but also will contribute to the broader question of how organisms represent quantitative information in their environment and use it to guide their behavior.

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