How Much Does Number Matter to a Monkey *(Macaca mulatta)*?

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Although many animal species can represent numerical values, little is known about how salient number is relative to other object properties for nonhuman animals. In one hypothesis, researchers propose that animals represent number only as a last resort, when no other properties differentiate stimuli. An alternative hypothesis is that animals automatically, spontaneously, and routinely represent the numerical attributes of their environments. The authors compared the influence of number versus that of shape, color, and surface area on rhesus monkeys' *(Macaca mulatta)* decisions by testing them on a matching task with more than one correct answer: a numerical match and a nonnumerical (color, surface area, or shape) match. The authors also tested whether previous laboratory experience with numerical discrimination influenced a monkey's propensity to represent number. Contrary to the last-resort hypothesis, all monkeys based their decisions on numerical value when the numerical ratio was favorable.

Keywords: numerosity, numerical cognition, Weber's law, nonhuman primates

In many studies, researchers have established that nonhuman animals have a fundamental capacity for nonverbally estimating the numerical value of a set of objects (e.g., Beran, Beran, Harris, & Washburn, 2005; Brannon & Terrace, 1998, 2000; Cantlon & Brannon, 2005, 2006a, 2006b; Emmerton, 1998; Hauser, Tsao, Garcia, & Spelke, 2003; Meck & Church, 1983; Washburn & Rumbaugh, 1991). In fact, nonhuman animals possess a capacity for roughly enumerating and comparing numerical stimuli, such as arrays of dots and sequences of tones, that is comparable to that of adult humans (e.g., Cantlon & Brannon, 2005, 2006a; Whalen, Gallistel, & Gelman, 1999). Both animals and humans discriminate nonsymbolic numerical stimuli according to the constraints of Weber's (1851/1966) law, whereby successful discrimination of two numerical values depends on their ratio. For example, both animals and humans are faster and more accurate at comparing four dots to eight dots (a 1:2 ratio) than comparing four dots to six dots (a 2:3 ratio) because the ratio of four to eight is easier to discriminate than that of four to six.

Recently, we directly compared rhesus monkeys' *(Macaca mulatta)* and adult humans' performance on the same nonverbal numerical task and found qualitative and quantitative similarities in their response patterns (Cantlon & Brannon, 2006a). Monkeys and humans showed parallel ratio-dependent numerical performance both in accuracy and response time on an ordinal numerical task. Overall, humans were more accurate than were monkeys; however, humans also responded more slowly, reflecting a possible difference between the speed–accuracy trade-off thresholds of monkeys and humans.

In other studies of numerical cognition in monkeys, researchers have provided evidence of a spontaneous capacity for numerical estimation in untrained animals (e.g., Flombaum, Junge, & Hauser, 2005; Hauser, Carey, & Hauser, 2000; Hauser, Tsao, Garcia, & Spelke, 2003; Jordan, Brannon, Logothetis, & Ghazanfar, 2005; Santos, Barnes, & Mahajan, 2005; Uller, Hauser, & Carey, 2001). For example, Flombaum et al. (2005) found that semi-free-ranging rhesus monkeys track the number of objects that are placed behind a screen such that they will look longer when an occluder is lifted, revealing an unexpected number of items. Specifically, monkeys looked longer when they witnessed two groups of two lemons placed behind an occluder that was then lifted, revealing eight lemons, compared with when the occluder was lifted, revealing four lemons. Thus, monkeys appear to spontaneously form expectations about the number of lemons that pass behind an occluder and look longer at a display that violates their expectations. The fact that untrained monkeys spontaneously represented the numerical values of the sets suggests that number is a salient attribute of a set of items for monkeys in their natural environments.

However, there is a discrepancy in the literature between (a) studies evincing spontaneous numerical cognition in nonhuman animals using looking time as the dependent measure and (b) studies requiring animals to make explicit decisions on the basis of number, such as in operant laboratory tasks. Studies of spontaneous numerical cognition under seminatural conditions suggest that animals have a natural capacity to discriminate stimuli on the basis of their numerical values; however, studies that require animals to make explicit decisions about numerical values in the laboratory often require animals to undergo extensive training and specific stimulus manipulations before the animals reliably use the numerical attribute of stimuli to make explicit decisions (e.g., Brannon &

Terrace, 1998; Breukelaar & Dalrymple-Alford, 1998; Cantlon & Brannon, 2006a, 2006b; Nieder, Freedman, & Miller, 2002; but see Hauser, Carey, & Hauser, 2000). This discrepancy raises the question of why nonhuman animals require such extensive training for discrimination of numerical values if they already posses a natural ability and proclivity for doing so.

One possible explanation for the difference between laboratory studies and studies of untrained animals is that in laboratory tasks, researchers implement more rigorous controls for dimensions that can serve as cues to stimulus differences, such as time or cumulative surface, thereby increasing the demand for pure numerical representation. In several prior studies in which researchers set forth evidence of spontaneous numerical cognition in nonhuman animals, numerical value was confounded with nonnumerical dimensions such as cumulative surface area and/or total volume (e.g., Beran, 2001; Beran et al., 2005; Beran & Rumbaugh, 2001; Boysen & Bernston, 1989; Hauser, MacNeilage, & Ware, 1996; Suda & Call, 2005) and presentation rate (e.g., Hauser, Carey, & Hauser, 2000) in their stimuli. As such, the number of studies demonstrating pure numerical competence in untrained animals is limited (but, for potential exceptions, see Flombaum, Junge, & Hauser, 2005; Hauser, Tsao, Garcia, & Spelke, 2003). Therefore, the possibility remains that pure numerical ability only emerges in the laboratory after long training periods with controlled stimuli.

Indeed, many researchers have argued that numerical representation is invoked by animals only as a last-resort strategy (e.g., Breukelaar & Dalrymple-Alford, 1998; Davis, 1993; Davis & Memmot, 1982; Davis and Perusse, 1988; Seron & Pesenti, 2001). That is, animals represent the numerical value of a set only when there are no other salient dimensions on which they could base their decisions, such as when shape and color do not differ among the relevant stimuli. According to this view, animals have a capacity to represent number, but this capacity emerges only under certain conditions, specifically as a consequence of reward contingencies during laboratory training.

Support for the last-resort hypothesis comes from evidence that animals' numerical performance is only as accurate as a particular laboratory task demands. For example, in studies by Hurwitz (1962) and Platt and Johnson (1971), rats were required to make a specific number of presses on a lever to receive reinforcement. In both studies, rats were significantly more accurate when they were penalized for prematurely terminating their sequence of presses than when there was no penalty for prematurely ending the response sequence. The fact that rats' ability to accurately determine the number of responses required was highly sensitive to the reward contingencies of the task suggests that performance may have been influenced by external factors related to the task as opposed to the internal numerical competence of the individual animals.

There is also some evidence that animals preferentially represent nonnumerical stimulus properties, such as temporal duration, over number. In a study by Breukelaar and Dalrymple-Alford (1998), rats learned to use temporal properties much more readily than numerical properties when discriminating sequences of tones. When undergoing weeks of training to discriminate the number and duration of tones in a sequence, rats never exhibited the same level of performance on numerical discrimination trials as they did on temporal discrimination trials.

In another experiment, Breukelaar and Dalrymple-Alford (1998) found that even rats with extensive, successful numerical training base their decisions on time when number and time are in conflict. Rats were trained to press one lever in response to two-tone sequences ("few") and another lever in response to eight-tone sequences ("many"), with total sequence duration equated between the two kinds of sequences. Then, they were tested with ambiguous stimuli in which a sequence with two tones had a total duration of 8 s, whereas a sequence with eight tones had a total duration of 2 s. On the majority of trials, rats responded "few" when presented with the eight-tone, 2-s sequence and "many" when presented with the two-tone, 8-s sequence, indicating that rats were basing their decisions on the duration of the sequence as opposed to the number of tones in the sequence. Even having undergone extensive numerical training, rats apparently found it easier to use the temporal, rather than the numerical, properties of the sequences.

In agreement with the last-resort hypothesis, Seron and Pesenti (2001) reviewed the literature on numerical cognition in nonhuman animals and concluded that there is little evidence that animals represent numerical values spontaneously, automatically, or even naturally. These authors argued that studies evincing spontaneous numerical cognition in untrained animals failed to demonstrate whether animals truly use pure numerical representations to make decisions or whether they rely on nonnumerical dimensions such as size and intensity, in addition to number, when these cues distinguish stimuli. Seron and Pesenti (2001) argued further that in the extant data from laboratory studies, animals attend to number only when nonnumerical dimensions such as time, volume, and intensity are dissociated from numerical value. Thus, from current studies, number representation can be construed as a highly unnatural and hard-won process for a nonhuman animal.

A developmental parallel of the last-resort hypothesis in the animal literature is the long-standing hypothesis that infants and young children more readily encode continuous dimensions such as surface area, duration, and perimeter than they do number (e.g., Clearfield & Mix, 1999, 2001; Feigenson, Carey, & Spelke, 2002; Mix, 1999; Mix, Huttenlocher, & Levine, 2002; Mix, Levine, & Huttenlocher, 1997; Newcombe, 2002; Piaget, 1952; but see Brannon, Abbott, & Lutz, 2004). According to these studies, number is not a primary dimension that humans spontaneously represent early in development; many dimensions, including size, time, and surface area, are more primitive than number over the course of human development. Rather, in this view, infants and young children require specific developmental experiences, such as language acquisition, to represent numerical values (Mix, 1999). Nonhuman primates lack the developmental experiences that are often considered critical for numerical development in humans (e.g., Mix, 1999), and their proclivity for representing numerical values will provide an important test of this hypothesis.

In this study, we aimed to test the predictions of two opposing hypotheses on the cognitive significance of numerical processes for nonhuman animals: One hypothesis proposes that numerical discrimination is an automatic and spontaneous component of an animal's cognitive repertoire, whereas an opposing hypothesis proposes that numerical cognition is a laborious, last-resort cognitive strategy for nonhuman animals. Few studies have been designed to test between these hypotheses to determine the salience of number relative to other stimulus attributes (but see Breukelaar & Dalrymple-Alford, 1998; Meck & Church, 1983). In this study, we directly tested the prediction of the last-resort

hypothesis that animals represent numerical information only when alternative cues are unavailable.

Monkeys were tested with a matching task in which the numerical value of the stimuli was confounded with each of three other dimensions (color, surface area, and shape). Monkeys could use number or the other, confounded dimension (color, surface area, or shape) to successfully perform the matching task. On infrequent and nondifferentially reinforced probe trials, we pitted number against an alternative dimension (color, surface area, or shape) to test whether monkeys would use number or the alternative dimension to perform the matching task. For example, in training, a monkey would be given a sample of two red hearts and would then be tested with two choices: one stimulus that contained two red hearts (match) and a second stimulus that contained four blue hearts (nonmatch). On a probe trial, if the sample contained two red hearts, the choice would be between two blue hearts (correct number match) or four red hearts (correct color match). Further, we parametrically varied the ratio between the numerical values of the choices across trials to observe the influence of numerical salience on monkeys' propensity to represent number.

A second goal of the study was investigating the role of previous experience in monkeys' number-matching performance. To this end, we compared the performance of 3 monkeys who had undergone extensive laboratory training on numerical tasks with that of 1 monkey who had no prior numerical training in the laboratory. We were interested in whether number-experienced monkeys and number-naïve monkeys would show similar decision biases for matching on the basis of number, shape, color, and surface area.

Experiment 1

In the first experiment, we trained 3 number-experienced monkeys and 1 number-naïve monkey on a match-to-sample task in which the correct match was equal in number and also matched on a second nonnumerical dimension (i.e., shape, color, or surface area). Subsequently, we tested the monkeys on probe trials in which we pitted the initially confounded dimensions (number and shape, color, or surface area) against one another to determine which dimension monkeys with extensive numerical training would use as the basis for matching. On probe trials, one choice stimulus matched in number and the other matched in shape, color, or surface area.

In testing the number-naïve monkey, we aimed to examine the role of laboratory experience in the determination of whether number is a salient dimension for a nonhuman animal that has not undergone extensive laboratory training on number tasks. Although we would have preferred to conduct this experiment with a larger sample size of number-naïve monkeys, this option was not possible in our laboratory. However, information from 1 monkey with no laboratory experience is sufficient for testing the prediction of the last-resort hypothesis that nonnumerical stimulus dimensions are universally more salient than number for nonhuman animals.

Method

Subjects and Apparatus

Number-experienced subjects were 3 socially-housed adult female rhesus macaques (*Macaca mulatta*) named Feinstein, Mikul-

ski, and Schroeder. All 3 monkeys had extensive training on numerical tasks, including numerical matching and ordinal tasks, in our laboratory. We explicitly trained Feinstein, Mikulski, and Schroeder to order and match numerical values while ignoring the color, shape, element size, density, and cumulative surface area of the stimuli (see Cantlon & Brannon, 2005, 2006a, 2006b; Jordan & Brannon, 2006). The number-naïve monkey was a single monkey (Boxer) who had no prior laboratory training with numerical tasks. Boxer participated only in matching and serial memory tasks that contained color photographs of landscapes, people, and other animals; she was never trained to judge stimuli on any dimension other than identity, although color and shape are likely cues to identity. All experimental procedures were approved by an internal animal care and use committee.

Subjects were tested in sound-attenuated booths while seated in Plexiglas primate chairs fitted with a juice delivery system. Stimuli were presented on a 17-inch touch screen computer monitor fixed to the inside wall of the soundproof booth. A custom-built program written in RealBasic presented the stimuli and registered responses. Stimuli were presented on a 3×2 touch screen matrix such that the spatial positions of the stimuli on the screen were randomly selected from six possible ports.

Task and Procedure

Monkeys were trained on a delayed match-to-sample task in which a sample was presented on the screen and, when the monkey pressed the sample, a 1-s delay ensued, followed by two test stimuli. On standard trials, one stimulus matched the sample in number and a second dimension (color, shape, or cumulative element size), and a second stimulus differed from the sample on both dimensions. If the monkey selected the matching stimulus, she was rewarded with 0.3 ml of Kool-Aid and received positive visual feedback (a 1-s pink screen) and auditory feedback (a 1-s chime). If the monkey selected the distractor stimulus, she received no Kool-Aid and, instead, a 3-s timeout ensued, and she received negative visual feedback (a 3-s black screen) and auditory feedback (a 1-s warning tone).

On probe trials, one stimulus matched the sample in number, and the second test stimulus matched in an alternative dimension. Subjects were rewarded with juice and with positive visual and auditory feedback, regardless of which of the two choice stimuli they selected on these probe trials. Throughout the experiment, trials were separated by a variable 2-s to 4-s intertrial interval. To decrease variability in the reaction time to touch the experimental stimuli, we required monkeys to initiate each trial by pressing a start stimulus, which was represented by a small black square in the center of the screen.

Before participating in this experiment, all 4 monkeys were trained on the delayed match-to-sample task to a performance criterion of 70%, with photographic stimuli for demonstration of proficiency with the general features of the task. The experimental stimuli consisted of visual arrays of elements as shown in Figure 1. Monkeys were tested in three different conditions: number versus shape, number versus surface area, and number versus color. To control for order effects, we presented each of the 4 monkeys with the three test conditions in a different order and subsequently tested them for a second round in the reverse order, such that each condition was tested twice for each monkey. Each
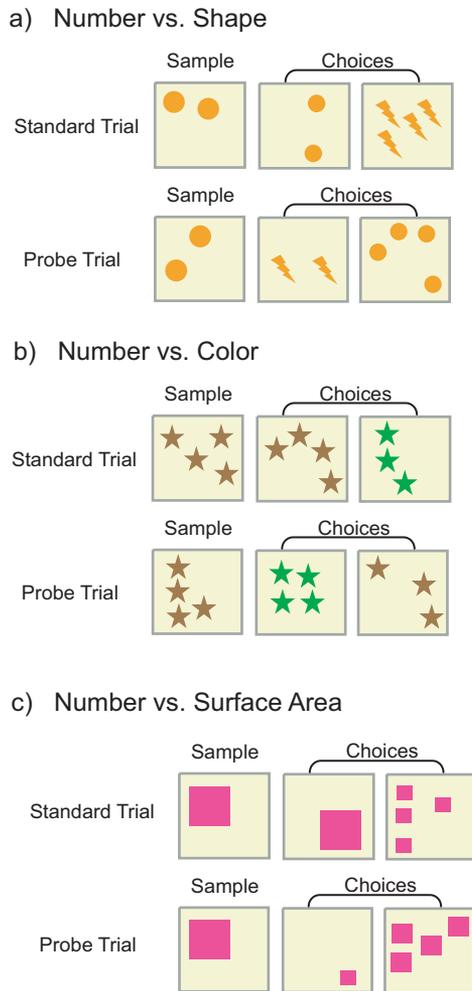
a) Number vs. Shape

b) Number vs. Color

c) Number vs. Surface Area

Figure 1. Relationships among the sample and choice stimuli on standard and probe trials for the three experimental conditions. a: In the number versus shape condition, on standard trials, one of the two choice stimuli matched the sample in both shape and number of elements whereas the second choice differed in both of these dimensions. On probe trials, shape and number were pitted against one another such that one of the choice stimuli matched the probe in shape but the other choice stimuli matched in number. b: On standard trials in the number versus color condition, one choice matched the sample stimulus in number and color whereas the other choice stimulus differed along both dimensions. On probe trials, one stimulus matched the sample in color while the other matched in number. Similarly, on the number versus surface area condition (c), on standard trials, one stimulus matched the sample in both cumulative surface area and number whereas the other choice matched in neither of these two dimensions. On probe trials, one choice stimulus matched the sample in cumulative surface area whereas the other choice matched in number.

condition included standard trials, in which the two dimensions were confounded and, thus, always predicted the same response, and probe trials, in which the two dimensions were pitted against one another and, thus, predicted different responses. Monkeys were trained to a 70% accuracy criterion on standard trials in each condition before probe trials were introduced. During sessions that included probe trials, 88% of trials consisted of standard trials and 12% were probe trials.

Each monkey completed approximately 200 probe trials and 1,800 standard trials per condition, combined across the two iterations of each condition. The presentation of probe trials was random except that a probe trial could not appear within the first 20 trials of a given session. The chance probability of a response to a given stimulus was .5 for both standard and probe trials.

Stimuli

The stimuli were trial-unique exemplars of the numerosities 1–4. Elements were randomly located within yellow 9 cm $\times$ 7.5 cm rectangles. The 12 possible sample/match–distractor permutations of the numerosities 1 through 4 (1–2, 2–1, 1–3, 3–1, 1–4, 4–1, 2–3, 3–2, 2–4, 4–2, 3–4, 4–3) occurred with equal frequency.

Number versus shape (Figure 1a). On standard trials, the sample and match were identical in both their number of elements and the local shape of the elements (1 of 15 different shapes), whereas the distractor stimulus was different from the sample stimulus and the match stimulus in both the number of elements and the local element shape. On probe trials, one choice stimulus matched the sample in its number of elements but not in local element shape, whereas the other choice stimulus matched the sample in its local element shape but not in its number of elements. Element size varied between the sample and choice stimuli but was equated between the two choice stimuli. Element color was constant among all three stimuli on a given trial.

Number versus color (Figure 1b). On standard trials, the sample stimulus and the match were identical in their color (one of nine colors) and number of elements, whereas the distractor differed in both of these dimensions. On probe trials, one choice stimulus matched the sample in its number of elements but not in the color of the elements, whereas the other choice stimulus matched the sample in element color but not in number of elements. Element size and shape were held constant for the sample and two choice stimuli.

Number versus surface area (Figure 1c). On standard trials, the sample stimulus and the match were identical in both their number of elements and the cumulative surface area (one of six different values: 1,200 total pixels; 2,400 total pixels; 3,600 total pixels; 4,800 total pixels; 6,000 total pixels; and 7,200 total pixels) of the elements, whereas the distractor differed from the sample and match in both of these dimensions. On probe trials, one choice stimulus matched the sample in the number of elements but not in the cumulative surface area of the elements, and the other choice stimulus matched the sample in cumulative surface area but not in number. Element shape and color were constant across the sample and choice stimuli on each trial.

Results and Discussion

Number-Experienced Monkeys

The performance of the number-experienced monkeys demonstrated that even in a situation in which it is not necessary for the monkey to represent number to solve a task, number is, in fact, represented by monkeys. In each of the three conditions, monkeys performed significantly above chance on standard trials (single sample t tests of accuracy on 12 match–distractor number pairs), number versus shape: $t(11) = 26.89$, $p < .001$; number versus

color: $t(11) = 14.62$, $p < .001$; number versus surface area: $t(11) = 7.17$, $p < .001$.[1] There was also a significant effect of numerical ratio (smaller number/larger number) on standard trial accuracy for each of the 3 monkeys in each of the three conditions (see Figure 2a; $N = 12$ match–distractor number pairs), $rs < -.63$, $ps < .05$, except for 1 monkey (Schroeder) on the number versus surface area condition, who showed a nonsignificant trend of the numerical ratio effect, $r = -.50$, $p = .09$. Thus, as the ratio in numerical value between the choice stimuli decreased, accuracy on standard trials increased. This result indicates that numerical value influenced the monkeys' performance even though monkeys could have ignored number and attended solely to color, shape, or surface area to select the match.

On probe trials, number was pitted against a second dimension, and monkeys were positively reinforced, regardless of whether they chose the numerical or nonnumerical match. Response time on probe trials was significantly slower than on standard trials (755 ms vs. 592 ms), $t(11) = 4.50$, $p < .05$, suggesting that the dissociation of the two dimensions affected performance. For each monkey, in each of the three conditions, the probability of making a number match was modulated by the numerical ratio between the choice stimuli (see Figure 2b; $N = 12$), $rs < -.63$, $ps < .05$; the probability of making a numerical match increased as the ratio between the choice stimuli decreased.

Figure 2b illustrates that at the most difficult ratio (.75), monkeys were more likely to match on the basis of color and shape than on the basis of number, binomial tests versus 0.5 (chance), $ps < .05$, and 2 of the 3 monkeys were more likely to match on the basis of cumulative surface area than on the basis of number, Schroeder: $p = .02$, Mikulski: $p = .01$, whereas the remaining monkey (Feinstein) showed no bias relative to chance, $p = .14$. At the easiest numerical ratio (.25), 1 monkey (Mikulski) was significantly biased to match on the basis of number over shape, binomial test versus 0.5 (chance), $p = .0003$, whereas 2 monkeys showed no bias toward shape or number at this ratio, Feinstein: $p = .12$; Schroeder: $p = .09$. All monkeys were significantly more likely to match on the basis of number than on the basis of color ($ps < .006$) or surface area ($ps < .000001$) at this ratio. Thus, when numerical ratio was small and number was easy to discriminate, monkeys typically preferred number as a basis for matching to the alternative stimulus dimensions tested. Further, for the number versus surface area condition, each monkey had a significant overall bias toward selecting the numerical match (binomial tests), Feinstein: $p = .01$, Mikulski: $p = .03$, Schroeder: $p = .001$.

The fact that number influenced accuracy on standard trials for all three conditions suggests that monkeys attend to the numerical attribute of the stimuli without being explicitly rewarded for numerical discrimination. On probe trials, numerical ratio greatly influenced monkeys' propensity to make a numerical or nonnumerical match. Shape and color were more salient than number at large numerical ratios, when number was difficult to discriminate, whereas number was more salient than color at small numerical ratios, and, for 1 monkey, number was more salient than shape at small ratios. Monkeys rarely exhibited a strong bias to choose the cumulative surface area match over the number match on probe trials. Instead, each monkey exhibited an overall bias for matching on the basis of number over surface area across all numerical ratios.

All 3 number-experienced monkeys had extensive experience in numerical ordering (2 monkeys) and numerical matching tasks (all 3 monkeys) before this experiment. Our results clearly indicate

that number can be equally salient to color, shape, and surface area when number is easy to discriminate, but it is unclear to what degree this result depends on the monkey's training history.

Number-Naïve Monkeys

The performance of the number-naïve monkey exhibited key similarities with that of the number-experienced monkeys. The number-naïve monkey performed significantly above chance on the standard trials for all three conditions, single sample t tests of accuracy across 12 number pairs versus .5 (chance), number versus shape: $t(11) = 22.62$, $p < .001$; number versus color: $t(11) = 35.75$, $p < .001$; number versus surface area, $t(11) = 7.01$, $p < .001$. On two of the three conditions, the number-naïve monkey showed a significant numerical ratio effect on accuracy for standard trials (see Figure 2c; $N = 12$ number pairs), number versus shape: $r = -.72$, $p < .01$; number versus surface area: $r = -.80$, $p < .05$. On the third condition (number vs. color), there was a nonsignificant trend of increasing accuracy with decreasing numerical ratio, $r = -.32$, $p = .31$. Thus, numerical ratio influenced the number-naïve monkey's matching performance even when number was confounded with an alternative stimulus dimension, suggesting that despite having no prior experience performing numerical tasks, this monkey, similar to the number-experienced monkeys, represented the numerical value of the arrays.

On probe trials, the number-naïve monkey differed from the number-experienced monkeys in that she showed a significant bias for choosing color and shape over number as the basis for matching at every numerical ratio (see Figure 2d), binomial tests versus 0.5 (chance), $ps < .05$, whereas she chose number over surface area at the easiest numerical ratios, .25 and .33, $ps < .0001$. In the number versus surface area condition, at the most difficult numerical ratios, the number-naïve monkey showed a significant bias to match on the basis of cumulative surface area, .67 and .75, $ps < .05$.

Although the number-naïve monkey showed a tendency to select dimensions other than number during probe trials, her performance was clearly influenced by number because she showed a significant influence of numerical ratio on each of the three conditions ($N = 12$ number pairs in each condition), number versus shape: $r = -.74$, $p < .01$; number versus color: $r = -.69$, $p < .01$; number versus surface area: $r = -.81$, $p < .01$. Finally, similar to the number-experienced monkeys, the number-naïve monkey was slower on probe trials than on standard trials (861 ms vs. 808 ms), but this difference was not significant.

Comparison of Number-Experienced and Number-Naïve Monkeys

To compare the results of the probe trials between the number-experienced monkeys and the number-naïve monkey, we performed an analysis of variance for Experience (experienced, naïve) × Condition (shape, color, surface area), with average accuracy for each of the 12 number pairs as the dependent measure. This analysis revealed

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[1] Our primary analyses in all of these experiments focused on accuracy and the probability of making numerical matches. Although response time during correct trials is another typical dependent measure for numerical tasks, it is difficult to make predictions of response time patterns for this task because of the compound nature of the stimuli and the presence of more than one correct answer on each trial.
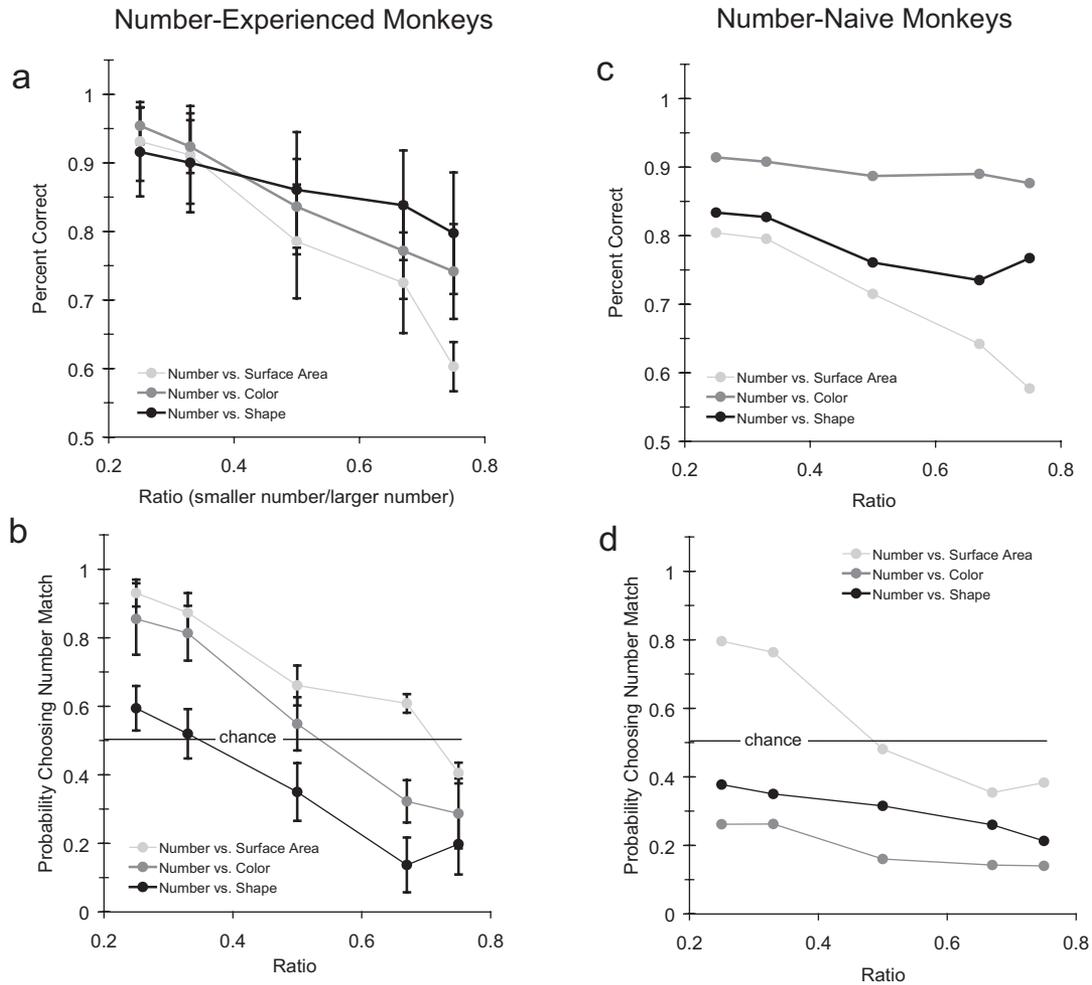
Number-Experienced Monkeys

a

b

Number-Naive Monkeys

c

d

Figure 2. Performance of number-experienced monkeys on the three experimental conditions (number vs. shape, number vs. color, and number vs. surface area) during standard trials (a) and probe trials (b) as a function of the ratio between the numerical values of the two choice stimuli. On standard trials (a), accuracy for choosing the matching stimulus is plotted. For probe trials (b), the probability of choosing a numerical match is plotted (chance = .5). Standard error bars reflect variance between the three monkeys. Performance of number-naive monkey on the three experimental conditions (number vs. shape, number vs. color, and number vs. surface area) was a function of numerical ratio. On standard trials (c), accuracy for choosing the matching stimulus is plotted. For probe trials (d), the probability of choosing a numerical match is plotted (chance = .5).

main effects of experience, $F(1, 22) = 8.86$, $p < .01$, and condition, $F(2, 44) = 55.04$, $p < .001$, as well as an Experience × Condition interaction, $F(2, 44) = 16.36$, $p < .001$. We examined these effects via Fisher's least significant difference post hoc tests.

The main effect of experience resulted from the number-experienced monkeys' greater overall propensity to make a numerical match compared with the number-naive monkey across all conditions and numerical pairs (.53 vs. .35). The main effect of condition was due to both groups of monkeys showing a higher probability for making a number match in the surface area condition (.61) than for making a number match in either of the other two conditions (.33 and .37 for shape and color, respectively). Finally, the Experience × Condition interaction (parsed with Fisher's least significant difference post hoc tests) resulted from a significant difference between number-experienced and number-

naïve monkeys in the probability of making a number match in the number versus color condition (.55 vs. .18, $p < .01$) but not in the number versus shape condition (.35 vs. .31, $p = .71$) or the number versus surface area condition (.68 vs. .54, $p = .20$). Thus, the number-naïve monkey was less likely, overall, to use number as a basis for matching than were the number-experienced monkeys; however, the number-naïve monkey's overall bias for choosing the numerical match did not differ significantly from that of the number-experienced monkeys in two of the three conditions.

Parametric Modulation of Performance by Cumulative Surface Area

Because differences in cumulative surface area, like differences in number, are easily quantified, we analyzed performance across

standard and probe trials as a function of the difference in cumulative surface area between the match and distractor for the number versus surface area condition for number-experienced and number-naïve monkeys. Both groups of monkeys showed increased accuracy as the difference in cumulative surface area between the match and distractor increased on standard trials ($N = 5$ cumulative surface area differences from six possible cumulative surface area values), number-experienced: $r = .88$, $p < .05$ (Feinstein); $r = .96$, $p < .01$ (Mikulski); $r = .98$, $p < .01$ (Schroeder); number-naïve: $r = .95$, $p < .05$ (Boxer). Thus, for cumulative surface area as well as for number, monkeys can match stimuli more easily when the values along these dimensions are more discriminable. This finding suggests that both the numerical and spatial extent of the stimuli exert control over monkeys' behavior, regardless of their previous experiences.

However, in probe trials, the influence of cumulative surface area on the performance of number-experienced and the number-naïve monkey differed. The number-naïve monkey was significantly more likely to match based on cumulative surface area as the difference between the match and distractor along this dimension increased ($N = 5$ area differences), $r = .93$, $p < .05$. In contrast, the number-experienced monkeys were less influenced by cumulative surface area on probe trials: Two monkeys showed no statistically significant increase in the likelihood of choosing the cumulative surface area match as the difference increased ($N = 5$ area differences), Feinstein: $r = .48$, $p = .4$, Schroeder: $r = .20$, $p = .8$, and 1 monkey (Mikulski) showed a significant effect, $r = .89$, $p = .04$. Thus, when number was pitted against cumulative surface area in probe trials, the number-naïve monkey was affected by cumulative surface area whereas the number-experienced monkeys primarily attended to the numerical relationships among the sample, match, and distractor.

This analysis reinforces the finding that cumulative surface area is not always a more salient dimension than number and that experience influences the salience of cumulative surface area relative to number. However, cumulative surface area can influence monkeys' decisions, perhaps more so for monkeys that have had no prior numerical training.

Experiment 2

To ensure that our results would generalize to a wider range of numerical values, we replicated the testing procedures of Experiment 1 with a larger range of numerical values (1–8) and tested 1 of the number-experienced monkeys and the number-naïve monkey from Experiment 1. Note that for this experiment, the number-naïve monkey still had never received differential reinforcement for discriminating numerical values.

Method

Subjects and Apparatus

Two socially-housed adult female rhesus macaques (*Macaca mulatta*) participated in this experiment: One was number-experienced (Schroeder), and 1 was number-naïve (Boxer). The apparatus was identical to that used in Experiment 1.

Task Procedure, Stimuli, and Data Analysis

The only difference in procedure from Experiment 1 was that stimuli were exemplars of the numerosities 1, 2, 3, 4, 6, and 8. All 30 possible permutations of these six numerosities were presented with equal frequency in standard and probe trials.

Results and Discussion

Number-Experienced Monkeys

Figure 3a shows that the pattern of decreasing accuracy with increasing numerical ratio held with the larger numerical range for the number-experienced monkey on standard trials ($N = 7$ numerical ratios), number versus shape: $r = -.87$, $p < .01$; number versus color: $r = -.86$, $p < .01$; number versus surface area: $r = -0.88$, $p < .01$, and on probe trials, number versus shape: $r = -.87$, $p < .01$; number versus color: $r = -.94$, $p < .01$; number versus surface area: $r = -0.98$, $p < .01$. On probe trials (see Figure 3b), this monkey showed a significant bias for matching on the basis of number at the easiest numerical ratios in each of the three conditions (.1 and .2 ratios), binomial tests versus .5 (chance), number versus shape: $p = .0008$; number versus color: $p = .002$; number versus surface area: $p = .00001$. Further, the number-experienced monkey was significantly more likely, overall, to choose number over surface area, averaged across all numerical ratios, binomial tests versus .5 (chance), $p = .0000001$. Thus, the response rules that monkeys used to perform this task with the small range of numerical values in Experiment 1 clearly generalized to a wider range of numerical values for this number-experienced monkey.

Number-Naïve Monkeys

Figure 3c shows that with the new range of values, the number-naïve monkey showed robust numerical ratio effects in accuracy for each of the three conditions on standard trials (see Figure 3c; $N = 7$ numerical ratios), number versus shape: $r = -.93$, $p < .01$; number versus color: $r = -.97$, $p < .01$; number versus surface area: $r = -.96$, $p < .01$. Thus, the trends obtained in Experiment 1 for the number-naïve monkey were even more apparent with the expanded numerical range. Because no differential reinforcement was used on probe trials in Experiment 1, the robust numerical ratio effect reported for the expanded numerical range provides compelling evidence that numerical value can be represented by a monkey that has not undergone number training.

Figure 3d shows that on probe trials, the number-naïve monkey was increasingly likely to choose the numerical match over the nonnumerical match as the numerical ratio between the choice stimuli decreased in all three conditions ($N = 7$ ratios), number versus shape: $r = -.94$, $p < .01$; number versus color: $r = -.82$, $p < .05$; number versus surface area: $r = .87$, $p < .05$. At the easiest numerical ratios, the numerical match was selected significantly more often than was the shape match or surface area match (.1 and .2 ratios), binomial tests versus .5 (chance), number versus shape: $p = .03$; number versus surface area: $p = .000003$; however, the color match was selected significantly more often than was the number match, even for these small numerical ratios, number versus color: $p = .005$. Further, similar to the number-experienced monkey, the number-naïve monkey had an overall bias for selection of the numerical match over the cumulative surface area match, averaged across all ratios tested, binomial test versus .5 (chance), $p = .02$.
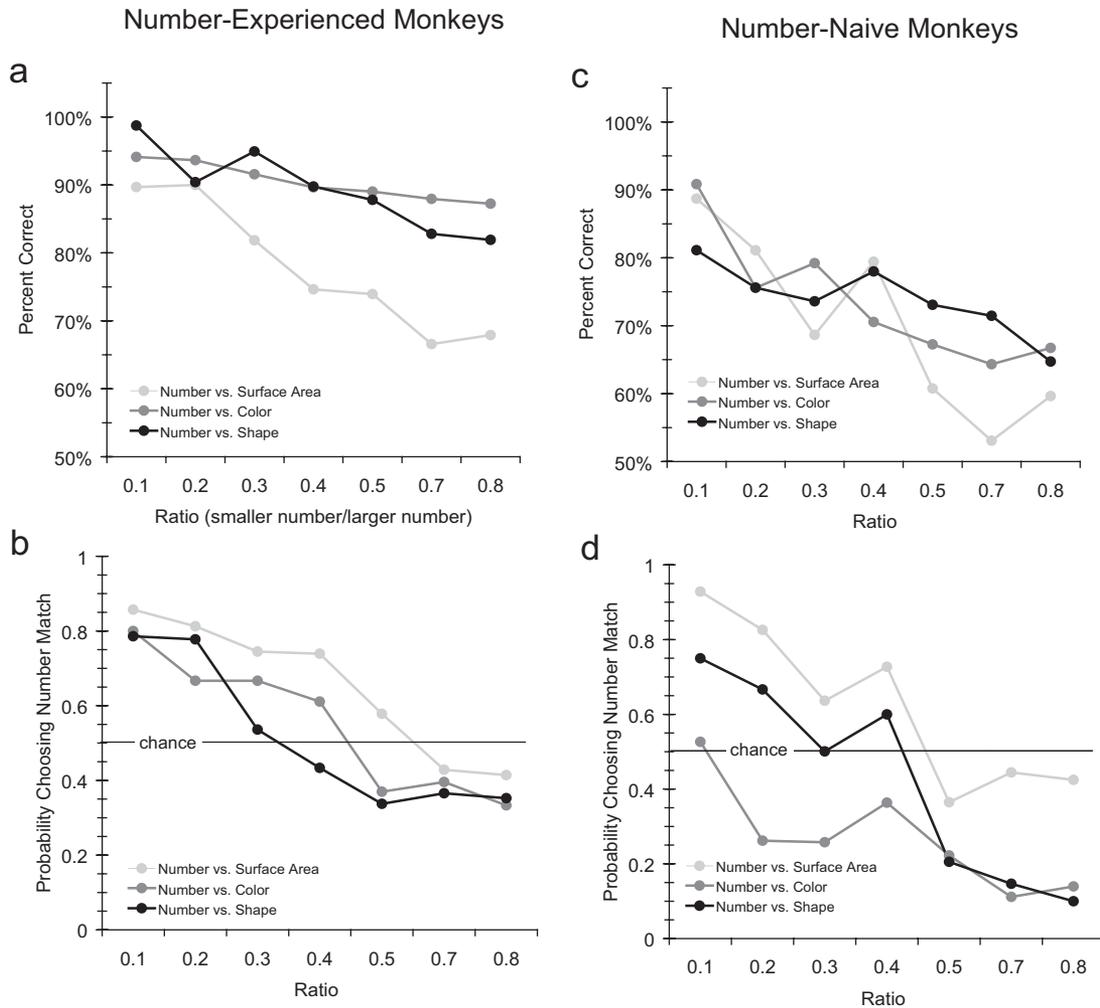
Number-Experienced Monkeys

Number-Naive Monkeys

Figure 3. Performance of one number-experienced monkey tested with an expanded range of numerical values ranging from 1 to 8 plotted by numerical ratio for standard trials (a) and probe trials (b). Performance of number-naïve monkey on sessions included an expanded range of numerical values ranging from 1 to 8 plotted by numerical ratio for standard trials (c) and probe trials (d).

The performance of the number-naïve monkey on this expanded range of values was consistent with her performance in Experiment 1 and also highlights striking parallels with the performance of the number-experienced monkey. Color was typically more salient than number for the number-naïve monkey; however, at small numerical ratios, number was more salient than both shape and cumulative surface area. Furthermore, the number-naïve monkey's performance was affected by number on standard and probe trials in all three conditions, as reflected by the numerical ratio effect on her performance.

General Discussion

A common view of the numerical abilities of nonhuman animals has been that extensive laboratory training produces artificial numerical competence that is not in the natural repertoire of animals (Breukelaar & Dalrymple-Alford, 1998; Davis, 1993; Davis & Memmott, 1982; Davis & Perusse, 1988; Seron & Pesenti, 2001).

This view, referred to as the last-resort hypothesis, has been supported by evidence that the numerical performance of animals is highly sensitive to reward contingencies and the richness of the stimuli. Contrary to this view, we found that when number-experienced monkeys performed a task in which they were not required to represent numerical values, their performance was, nevertheless, strongly influenced by number. We also found that a monkey with no previous training on number tasks spontaneously represented number when the numerical ratio was sufficiently discriminable, despite the fact that this was not a task requirement.

Perhaps most compelling is our finding that both number-experienced monkeys and number-naïve monkeys exhibited a stronger bias for basing their task decisions on number than on cumulative surface area. When number was pitted against cumulative surface area in probe trials, number-experienced monkeys actually showed little influence of cumulative surface area on their performance. Previous training in which monkeys learned to base

their decisions on number and ignore continuous variables, no doubt, encouraged the monkeys to ignore surface area and attend only to number in the current experiment. Although the number-naïve monkey's performance showed a greater influence of cumulative surface area than did the performance of the number-experienced monkeys, number was more salient than area for this monkey at highly discriminable numerical ratios.

In studies conducted with human infants and children, researchers have suggested that the ability to represent continuous dimensions such as surface area, duration, and perimeter may be more primary during development than the ability to represent number (e.g., Clearfield & Mix, 1999, 2001; Feigenson, Carey, & Spelke, 2002; Mix et al., 2002; Newcombe, 2002). In many of these studies, the authors used looking time, rather than explicit choice behavior, as the dependent measure. Therefore, the methodological difference between studies of nonhuman animals that require extensive laboratory training and those that assess spontaneous cognition via looking time measures is unlikely to be the main explanation for the discrepant reports of animals' proclivity for representing numerical value from these two different methods. However, one caveat to this conclusion is that in recent studies, researchers have challenged the notion that human infants always attend to continuous variables in lieu of number (see Brannon, Abbott, & Lutz, 2004). Perhaps human infants, similar to nonhuman animals, spontaneously represent numerical value rather than cumulative surface area at easy numerical ratios, even when cumulative surface area differentiates stimuli in addition to number.

One nonnumerical dimension that was not tested against number in this study is the overall density of the elements. Although it is possible that monkeys represented density rather than number to perform the matching task, previous studies from our laboratory have shown that monkeys' performance is unaffected when density is not a reliable cue to number (Cantlon & Brannon, 2006a), even when monkeys have no prior training with density-controlled stimuli (Jordan & Brannon, 2006). Thus, it seems unlikely that monkeys used density, rather than numerical value, as a basis for judgment in this task.

Collectively, the results of these two experiments suggest that numerical value is a salient stimulus dimension for a monkey, regardless of task demands or prior training. However, our results also suggest that prior training on numerical tasks enhances the salience of the numerical dimension. As expected, number-experienced monkeys were more likely to use number as a basis for matching than was the number-naïve monkey. The previous numerical training of the number-experienced monkeys included an almost identical numerical matching task, which may have exaggerated the effect of prior training on numerical performance in this study. It would be of interest for researchers to assess performance on this numerical matching task in monkeys with numerical ordering experience but no numerical matching experience.

Although the focus of this study was testing the hypothesis that monkeys will attend to the numerical attribute of stimuli to solve a task only when there is no alternative strategy available, an open question remains: To what extent does the relative discriminability of the nonnumerical dimension (e.g., shape, color, and area) affect monkeys' propensity for using number as a basis for matching? In our analysis of the effect of cumulative surface area on accuracy, we begin to address this question; however, a full investigation of this question requires parallel analyses for salience differences in color or shape. It is clear that monkeys discriminated the colors and shapes of the elements from their biases to use these dimensions, instead of number, as a basis for matching on a considerable proportion of trials; however, it is unclear how the range of color and shape values subjectively map on to the numerical values that we tested. An important next step would be establishing discrimination thresholds for number, shape, color, and area and comparing a monkey's propensity to match stimuli on the basis of number or an alternative dimension when the values compared are at an equal just noticeable difference.

In many studies, researchers have provided evidence of parallels between the numerical abilities of humans and nonhuman animals (e.g., Brannon & Roitman, 2003; Brannon & Terrace, 1998, 2000; Cantlon & Brannon, 2005, 2006a; Emmerton, 1998; Hauser, Tsao, Garcia, & Spelke, 2003; Meck & Church, 1983; Whalen, Gallistel, & Gelman, 1999). In other studies, researchers have used indirect measures of knowledge such as looking time, reaching location, and reaching time to show that nonhuman primates spontaneously represent number (e.g., Flombaum, Junge, & Hauser, 2005; Hauser, Carey, & Hauser, 2000; Hauser et al., 2003; Jordan et al., 2005; Lewis, Jaffe, & Brannon, 2005; Santos, Barnes, & Mahajan, 2005). In our study, we add that number is a dimension that monkeys spontaneously use to inform explicit decisions, even when alternate dimensions are available. Thus, a proclivity for numerical representation may be another parallel between human and nonhuman numerical cognition.

In several studies, researchers have provided evidence that adult humans spontaneously and even automatically represent and have difficulty inhibiting their access to numerical information (e.g., Dehaene, 1997; Dehaene, Bossini, & Giraux, 1993; Lefevre, Bisanz, & Mrkonjic, 1988; Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004). Our finding that numerical ratio influenced both number-experienced and number-naïve monkeys' performance, even when they opted to match based on a nonnumerical stimulus dimension such as color and shape in probe trials, raises the possibility that monkeys, similar to humans, automatically represent the numerical values of sets of objects.

In summary, the argument that number is a last-resort representation for nonhumans is not supported by our data. Numerical training increases the salience of number, but monkeys do not require training to represent and attend to numerical value. Rather, monkeys represent number without prompting, and the subjective difference between numerical values determines whether or not number is selected as the basis for decision making. This fact is inconsistent with the last-resort hypothesis and, instead, supports the argument that monkeys and other animals naturally represent numerical values. Accordingly, the argument that numerical competence in nonhuman animals is an artificial result of extensive laboratory training must be disregarded.

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