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Weber's Law influences numerical representations in rhesus macaques (*Macaca mulatta*)

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Abstract We present the results of two experiments that probe the ability of rhesus macaques to match visual arrays based on number. Three monkeys were first trained on a delayed match-to-sample paradigm (DMTS) to match stimuli on the basis of number and ignore continuous dimensions such as element size, cumulative surface area, and density. Monkeys were then tested in a numerical bisection experiment that required them to indicate whether a sample numerosity was closer to a small or large anchor value. Results indicated that, for two sets of anchor values with the same ratio, the probability of choosing the larger anchor value systematically increased with the sample number and the psychometric functions superimposed. A second experiment employed a numerical DMTS task in which the choice values contained an exact numerical match to the sample and a distracter that varied in number. Both accuracy and reaction time were modulated by the ratio between the correct numerical match and the distracter, as predicted by Weber's Law.

Keywords Numerical competence · Nonhuman primate · Bisection · Weber's Law

Introduction

Research over the last 100 years has compellingly demonstrated that many different nonhuman animal species represent number independent of non-numerical stimulus dimensions (e.g., Boysen and Berntson 1989; Brannon and Terrace 1998; Emmerton et al. 1997; Hauser et al. 2003; Matsuzawa 1985; Meck and Church 1983; Nieder et al. 2002; Otlhof and Roberts 2000; Pepperberg and Gordon 2005; Roberts 2005). An analog magnitude system has

been proposed to underlie many of the numerical abilities of nonhuman animals (e.g., Beran 2004; Beran and Beran 2004; Beran and Rumbaugh 2001; Brannon and Roitman 2003; Brannon and Terrace 1998; Feigenson et al. 2004; Gallistel and Gelman 1992; Hauser et al. 2003; Nieder et al. 2002). The signature property of this system is that it obeys Weber's Law: Discrimination between two quantities depends on their ratio. This system is also thought to underlie the nonverbal numerical judgments made by adult humans (e.g., Barth et al. 2006; Boisvert et al. 2003; Cantlon and Brannon 2005; Moyer and Landauer 1967; Pica et al. 2004; Whalen et al. 1999). Furthermore, previous research has revealed that under some circumstances, human infants also show ratio-dependent number judgments, suggesting that an analog magnitude system for representing number may be both evolutionarily and developmentally conservative (e.g., Lipton and Spelke 2003; Xu and Spelke 2000).

Weber's Law states that $\Delta I/I = C$, where ΔI is the increase in stimulus intensity to a stimulus of intensity I that is required to produce a detectable change in intensity and C is a constant. Thus, if an organism detects a change in a 20-lb weight when 4 lb is added, it would need an 8-lb increment to detect a change in a 40-lb weight. If Weber's Law holds for number judgments, then accuracy and latency to make numerical comparisons should depend on the ratio of the two numerical values compared. Under Weber's Law, one possibility for the format of nonverbal numerical representations is that number is linearly scaled in psychological space, with the variability in a given numerical representation linearly increasing with the magnitude of the representation. This is referred to as scalar variance and has been argued by Gibbon, Meck, and Church to hold for both the representation of time and number in nonhuman animals (e.g., Gibbon 1977, 1981, 1986; Meck and Church 1983). An alternative explanation is that number might be logarithmically scaled in psychological space such that the psychological distance between 4 and 6 is smaller than the psychological distance between 2 and 4 (Dehaene and Changeux 1993; Dehaene 1997; Nieder and Miller 2003). Because both hypotheses predict that Weber's Law will hold for numerical judgments, no

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current data can definitively discriminate between these two alternatives (but see Brannon et al. 2001; Dehaene 2001).

The main method used to demonstrate that Weber's Law holds for number judgments in primates has been an ordinal comparison task. In this task, a subject is required to choose the numerically smaller or larger of two arrays. Typically, accuracy increases and latency to respond decreases as the difference between the two values increases (Beran 2001, 2004; Beran et al. 2005; Brannon and Terrace 1998, 2000; Judge et al. 2005; Nieder and Miller 2004; Rumbaugh et al. 1987; Smith et al. 2003; Washburn and Rumbaugh 1991). One primary method widely used to show that the numerical judgments made by rats and pigeons are modulated by Weber's Law is the bisection task, in which animals are trained to discriminate a small and large anchor numerosity and are then tested with intermediate values. The intermediate value probe trials require subjects to make a relative similarity judgment about whether the sample is closer to the small or large anchor value. Typically, the probability that an animal selects the large anchor value (the "choose large" response) increases with the test value. Furthermore, the test value for which the animals are indifferent and are equally likely to choose the small or large anchor—referred to as the point of subjective equality (PSE)—is generally found to be at the geometric mean of the anchor values in temporal and numerical bisection experiments (Church and Deluty 1977; Fetterman 1993; Meck and Church 1983; Meck et al. 1985; Platt and Davis 1983; Roberts 2005; Stubbs 1976). In addition, if Weber's Law holds for numerical judgments, then the psychometric functions that relate the probability of a "choose large" response to the test numerosity in a numerical bisection task should superimpose for different sets of anchor values with the same ratio. This has been shown to be true for temporal and numerical judgments in rats using successive auditory or visual arrays and in pigeons using both successive arrays and simultaneous visual arrays (e.g., Fetterman 1993; Gibbon 1986; Roberts 2005).

Here, we provide evidence that Weber's Law holds for numerical judgments in nonhuman primates using a delayed match-to-sample (DMTS) paradigm with a bisection procedure (Experiment 1) and an absolute numerical match procedure (Experiment 2). We first ask how a monkey's numerical judgments are impacted by non-numerical stimulus features such as cumulative surface area, contour length, and density. To explore this question, we employ an extensive set of stimulus controls and examine the effect of cumulative surface area, contour length, and density on accuracy when monkeys are required to match visual stimuli on the basis of numerosity. Secondly, we ask whether monkeys represent novel test values intermediate to two trained anchor values along a systematic ordinal numerical continuum. We do this by using a bisection task to examine whether the probability that a monkey will make a "choose large" response increases with the numerosity of sample values. Our third question is whether number representations of rhesus monkeys conform to Weber's Law. To test this, we first examine whether the psychometric functions that emerge from the bisection task superimpose when the

anchor values are varied in absolute value but maintain a constant ratio. We then examine whether accuracy and latency in a precise numerical matching task are modulated by the ratio of the correct choice to the distracter, as would be predicted by Weber's Law. The final question our research addresses is whether monkeys use a serial or parallel mechanism to determine the number of stimulus elements when tested with the simultaneous arrays. In the current paradigm, subjects control the duration of the sample and hence control the processing time for the sample. We therefore predict that if monkeys process the elements serially when forming numerical representations, then response time to the sample should increase with number.

Experiment 1A

In Experiment 1, three monkeys were trained to match novel exemplars of two trained anchor numerosities. In Experiment 1A, the anchor values were 2 and 8, whereas in Experiment 1B, the anchor values were 3 and 12. After establishing that the monkeys were able to match novel exemplars of these two numerosities based on number without relying on non-numerical cues such as element size, cumulative surface area, and density, the monkeys were tested in two bisection conditions in which the sample took on a wide range of values but the test was a forced choice between two trained anchor values.

Method

Subjects

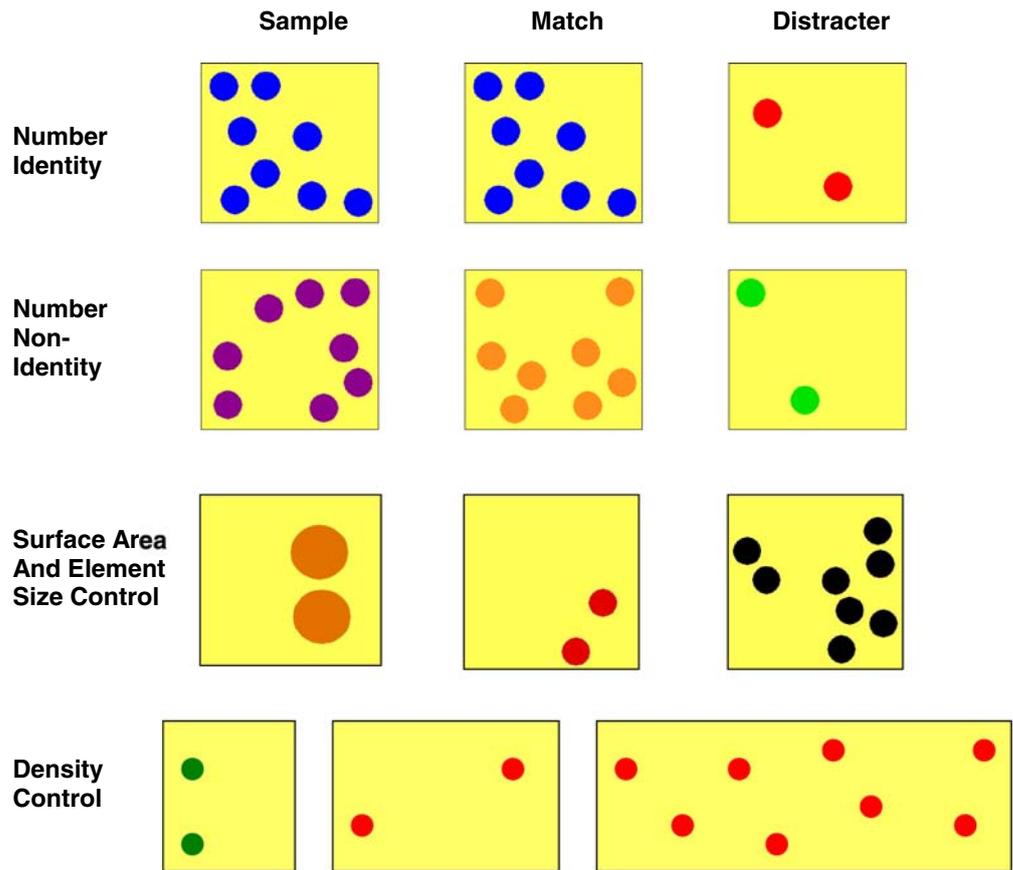
Subjects were three experimentally naïve female rhesus macaques (*Macacca mulatta*)—M, S, and F. All three subjects were approximately 6-years-old and were housed socially at Duke University in a Primate Products cage in a colony room with a 12:12-h light:dark cycle. Monkey chow was available *ad libitum* in their home cages; they also received daily foraging enrichment in these cages.

Apparatus

Monkeys were tested in small soundproof rooms constructed by Industrial Acoustics Company, Inc. Each subject was trained to sit in a primate chair and touch a touch-sensitive monitor mounted on the inside wall of the room. A Crist Instrument Company juice system was used to provide reinforcement through a juice spout, which was attached to the chair directly in front of the monkey's mouth.

A Dell OptiPlex GX400 computer executing a software program written in-house in JAVA was used to create, run, and control the sessions (i.e., to project stimuli onto the touchscreen) and to register responses. Experimenters could view an identical version of the monkey's screen on a second monitor attached to the master computer and view online summary statistics. The monkey's behavior was also monitored remotely by video.

Fig. 1 Examples of stimuli used in each of the four control conditions of the DMTS training tasks. The sample is depicted in the first column, with the match in the second and distracter in the third column. *Number identity*: The sample and match were identical. *Number non-identity*: The configuration and color of the elements differed between the sample and the match. *Surface area and element size control*: This specific example of stimuli shows a trial in which the cumulative surface area of the elements in the distracter was equal to that of the sample. On other trials, the cumulative surface area of the elements in the distracter was greater than or less than that of the sample. *Density control*: By no means exhaustive of the stimuli used in this control phase, the sample stimulus in this particular example has a greater density than the match and the same density as the distracter. On other trials, the sample density was equal to or less than the match density



Stimuli

Stimuli were yellow rectangles that contained a variable number of elements. The stimulus background varied in size to control for density (i.e., 10 cm × 2 cm, 10 cm × 8 cm, 10 cm × 10 cm, 10 cm × 16 cm, and 10 cm × 32 cm). The elements within each stimulus were circles that varied in diameter from 0.25 to 2.5 cm and color (green, red, blue, orange, purple, black). Elements within a stimulus were uniform in size and color. Additional details are provided later.

Procedure

Pretraining

Subjects were first trained to touch a static stimulus on the screen for juice reward. Once the monkeys responded rapidly to a single stimulus in any of the nine positions on the monitor, they proceeded through four phases of delayed match-to-sample training.

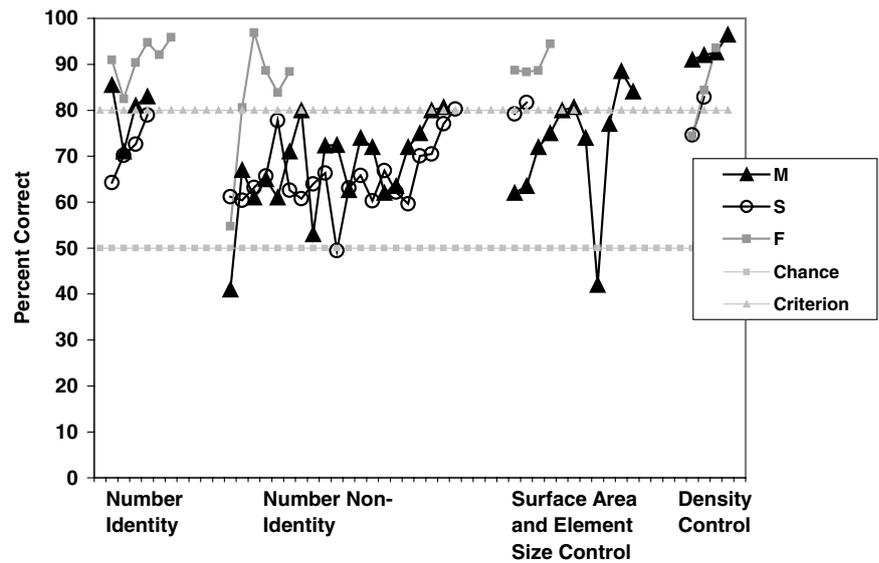
Training

To begin a trial, monkeys were required to press a red square located in the lower right corner of the screen. The sample stimulus then appeared in the center of the screen and re-

mained until the monkey touched it or until 10 s elapsed. Subsequently, two choice stimuli appeared immediately in two of the eight remaining screen locations. If the monkey correctly chose the match, a green border flashed for 700 ms around the match, a positive sound occurred, and a juice reward was delivered. In contrast, if the monkey touched the distracter, the screen turned black, a negative sound was emitted, and a 10-s time-out ensued. The inter-trial interval varied between 1 and 2 s. Monkeys were advanced to the next training phase after reaching a performance criterion of 80% accuracy on two consecutive days.

Training Phases 1–4 involved the numerosities 2 and 8 (examples of which are shown in Fig. 1). In Training Phase 1 (number identity DMTS), the sample and match were physically identical and the distracter elements always matched the sample in color and element size. In Training Phase 2 (number non-identity DMTS), all elements within the stimuli were uniform in size; however, the match and sample differed in both the configuration and color of the elements. The match and distracter always contained elements of the same size. Since element size was constant in Training Phase 2, the animal could have used cumulative dot area or contour length, rather than number, to match the stimuli. Thus, in Training Phase 3 (surface area and element size control), surface area and element size were controlled. In half of the trials, the cumulative surface area of the elements in the sample were equal to the cumulative surface area of the elements

Fig. 2 Three rhesus monkeys (M, S, and F) were trained on four phases of a DMTS task. Graphed here are their accuracies across these four phases. Also shown are the chance line of 50% and the criterion line of 80% accuracy. Data points for monkey S reflect averages for 5-session blocks



in the distracter while the match cumulative surface area varied; on the other half of trials a variety of cumulative surface areas were used such that sometimes the sample cumulative surface area was greater than, sometimes less than, and sometimes equal to the match cumulative surface area. Finally, on a subset of trials, the sample dot size was equal to the match dot size. In Training Phase 4 (density control), density was controlled by varying stimulus background size (the yellow rectangle on which the elements were placed) such that on one-third of trials the sample density equaled the match density, on a second third of trials the match density was greater than the sample density, and on the final third of trials the match density was less than the sample density. Throughout Training Phases 1–4, sessions lasted approximately 2.5 h, during which the monkeys completed anywhere from 30 to 1500 trials.

Bisection 1–9

After the monkeys learned to match 2 and 8 on the basis of numerosity, they were tested in a bisection procedure using the DMTS paradigm. Here, the sample was any value between 1 and 9 but the test was a forced choice between their two trained anchor values of 2 and 8. Seventy percent of trials were reinforced (positive or negative) and involved only the sample numerosities 2 and 8 to ensure the monkeys' continued participation. The remaining 30% of trials were unreinforced in that neither juice reward nor time-outs were delivered. Fifty percent of the unreinforced trials again presented the numerosities 2 and 8 as samples. On the remaining 50% of unreinforced trials (15% of all trials) the sample was an exemplar of the numerosity 1, 3–7, or 9.

Monkeys were tested on two unique stimulus sets, each for 3000 trials. The first set contained eight exemplars of each numerosity with all the stimulus controls described for Training Phase 4. In Stimulus Set 2, the color of the match and distracter was the same, while the color of the

sample was different from this color, making it impossible for the monkey to use color to perform above chance expectations. In addition, in one half of the Stimulus Set 2 trials, the cumulative surface area of the sample matched the cumulative surface area of the 2 in the choice stimuli, while on the other half of the trials, the cumulative surface area of the sample matched the cumulative surface area of the 8 in the choice stimuli. As in Stimulus Set 1, Stimulus Set 2 contained eight exemplars for each numerosity and testing continued for 3000 trials (51 session blocks).

Results and discussion

Acquisition

All three monkeys completed the four training phases and matched stimuli based on numerical equivalence regardless of continuous dimensions. As shown in Fig. 2, there was individual variation between monkeys in terms of the speed with which they progressed through the training phases; monkey F met the performance criterion in 2–6 sessions, while monkey M took 4–19 sessions and monkey S took 10–100 sessions. The largest performance decrement for all three monkeys occurred during the transition from the “number identity” training phase to the “number non-identity” training phase; after this transition, the monkeys could no longer base their choice on an exact identical match. Accuracy for all three monkeys was well above the chance level of 50% correct in the subsequent phases controlling for surface area, element size, and density—and in fact, two monkeys showed no performance decrement when moving to these phases.

In addition, to assess whether monkeys attended to continuous variables and whether these variables impacted numerical judgments, we analyzed accuracy as a function of whether continuous variables were congruent or incongruent with number during these training phases. On trials in

Table 1 Results of the effects of stimulus congruence and incongruence with number on accuracy in Experiment 1A

	SA congruence (%)	SA incongruence (%)	CL congruence (%)	CL incongruence (%)	D congruence (%)	D incongruence (%)
Overall accuracy	66.10 ± 5.00	63.90 ± 5.00	66.50 ± 7.30	65.90 ± 4.20	87.00 ± 6.50	89.80 ± 6.30
1st 100 trials	61.70 ± 4.90	59.20 ± 4.00	60.00 ± 5.00	61.40 ± 5.10	84.80 ± 7.20	84.20 ± 3.90
Last 100 trials	82.70 ± 7.80	78.70 ± 7.00	84.00 ± 9.60	85.30 ± 3.90	87.90 ± 6.10	91.20 ± 8.10

Note: Continuous variables represented include cumulative surface area (SA), contour length (CL), and density (D)

which number was considered congruent with cumulative surface area, the match contained both a larger number of elements and had a greater cumulative surface area than the distracter; conversely, on trials in which number was considered incongruent with cumulative surface area, a match containing a larger number of elements had a smaller cumulative surface area than the distracter. We also compared monkeys' accuracy during the first block of 100 training trials versus the last block of 100 training trials, to examine the effect of extended training.

Results of these analyses are shown in Table 1. A 2 (congruent versus incongruent) by 2 (first 100 trials versus last 100 trials) by 3 (continuous variable: Surface area versus contour length versus density) ANOVA showed no overall effect of stimulus congruence on accuracy [$F(1, 7) = 0.0009, p = 0.98$]. However, there was an overall main effect of trial block in that monkeys were significantly more accurate during the last 100 trials than during the first 100 trials: [$F(1, 7) = 7.52, p < 0.05$]. There were no other main effects or interactions.

Despite the fact that there was a statistical improvement from the first to the last 100 trials, all three monkeys performed above chance expectations in the first 100-trial block for all stimulus control conditions. One-sample t -tests were conducted for each monkey that compared accuracy for each of ten 10-trial blocks to chance when each continuous variable was congruent or incongruent with number (Monkey S, when each continuous variable was congruent (surface area: $t(9) = 10.25, p < 0.05$; contour length: $t(9) = 9.93, p < 0.05$; density: $t(9) = 23.24, p < 0.05$) or incongruent (surface area: $t(9) = 9.48, p < 0.05$; contour length: $t(9) = 8.13, p < 0.05$; density: $t(9) = 38.1, p < 0.05$) with number; Monkey M, when each continuous variable was congruent (surface area: $t(9) = 11.06, p < 0.05$; contour length: $t(9) = 9.22, p < 0.05$; density: $t(9) = 23.02, p < 0.05$) or incongruent (surface area: $t(9) = 10.40, p < 0.05$; contour length: $t(9) = 12.58, p < 0.05$; density: $t(9) = 37.21, p < 0.05$) with number; Monkey F, when each continuous variable was congruent (surface area: $t(9) = 11.31, p < 0.05$; contour length: $t(9) = 13.01, p < 0.05$; density: $t(9) = 24.09, p < 0.05$) or incongruent (surface area: $t(9) = 10.50, p < 0.05$; contour length: $t(9) = 11.87, p < 0.05$; density: $t(9) = 38.63, p < 0.05$) with number). Thus, all three monkeys used number and did not rely on continuous variables to perform above chance expectations in the first 100 trials.

Collectively, these data suggest monkeys did not extrapolate number as an absolute last resort, only once all possible confounding parameters were controlled, as suggested by Davis and Memmott (1982). Instead, the data are more con-

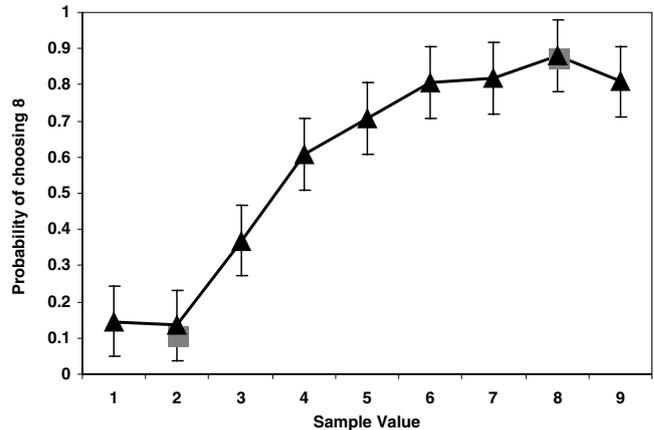


Fig. 3 The probability of choosing 8 (rather than 2) as a function of the numerical value of the sample in Experiment 1A. Data reflect averages over three monkeys and two stimulus sets. Triangles reflect data points from non-differentially reinforced probe trials, whereas squares represent reinforced trials with sample values 2 and 8

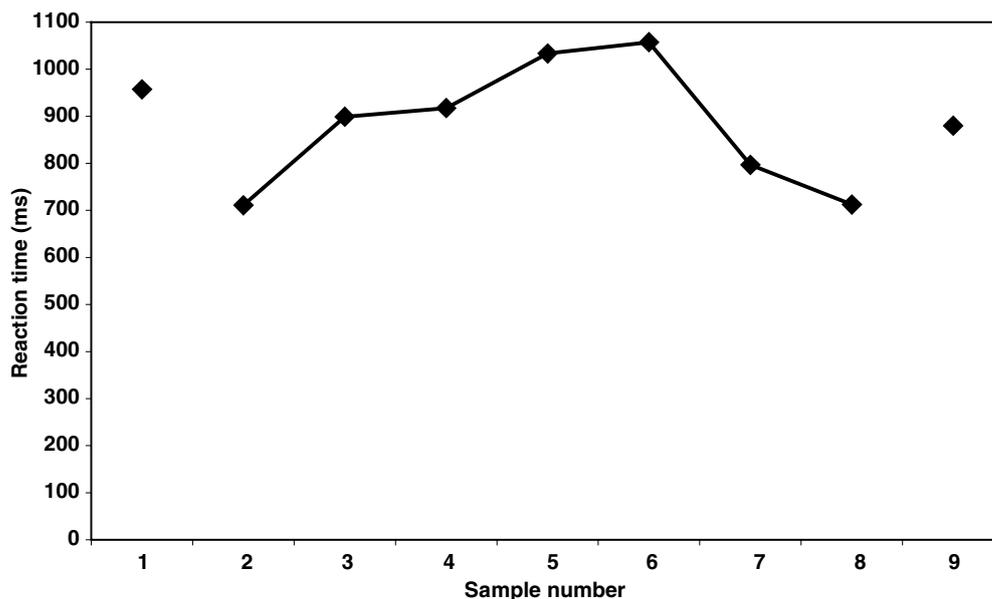
sistent with the idea that rhesus monkeys can match stimuli based on numerical equivalence, regardless of continuous dimensions that are often confounded with number.

Bisection

Figure 3 shows that when novel numerical values were presented as samples, the probability of choosing 8 increased with the numerosity of the sample for all monkeys (monkey S: $r^2 = 0.91, p < 0.05$; monkey M: $r^2 = 0.80, p < 0.05$; monkey F: $r^2 = 0.78, p < 0.05$). As shown in Fig. 3, the probability of choosing 8 when the sample values were 2 or 8 did not differ between reinforced and unreinforced trials. The data were fit with a cumulative normal distribution to determine the point of subjective equality, which was determined by the mean of the fit. A fit with the PSE at 3.8 ± 0.55 accounted for 92.7% of the variance.¹ The Weber fraction was 0.47 and was calculated by finding the ratio of the difference limen (half the difference between the numerosity corresponding to 75% choices of 8 and the numerosity corresponding to 25% choices of 8) to the PSE.

¹ Two out of three monkeys exhibited PSEs nearer to the geometric mean than the arithmetic mean (Monkey M, 3.51 and Monkey F, 3.04). Monkey S had a PSE of 4.86. We follow the convention of previous bisection studies in animals that have focused on group data/PSEs and have therefore not highlighted individual differences (Emmerton et al. 1997; Meck et al. 1985; Roberts and Mitchell 1994; Roberts 2005; Siegel 1986). Future studies with larger sample sizes should explore individual differences.

Fig. 4 Latency to choose a test stimulus as a function of sample number in Experiment 1A, averaged across all three subjects. Reaction time increases for sample numbers most intermediate to the trained anchor values and also for the two outside values of 1 and 9, and may reflect uncertainty



The general shape of the function did not change over time from Stimulus Set 1 to 2. However, the PSE was 4.16 for Stimulus Set 1 with a Weber fraction of 0.58, while the PSE was 3.5 for Stimulus Set 2 with a Weber fraction of 0.32, suggesting that precision increased over time. Single-sample *t*-tests were used to compare the PSEs observed for each monkey in each of these two stimulus sets to the arithmetic and geometric means of the anchor values. Results showed that these PSEs were not significantly different from the geometric mean [$t(5) = -0.729, p = 0.499$], but were significantly different from the arithmetic mean [$t(5) = -4.598, p < 0.05$].

The median reaction times to make a choice were determined for each monkey at each sample number; the average latency to respond across all three monkeys is shown as a function of sample number in Fig. 4. Specifically, reaction time generated an inverted U-shaped function and likely reflected subjects' uncertainty at intermediate values near the PSE and values outside the range created by the trained anchor points (second-order polynomial regression, $r^2 = 0.86, p < 0.05$).

Experiment 1B

Bisection 3–12

The same bisection task was used in Experiment 1B with the anchor values 3 and 12. This second set of absolute values was used to determine whether the shape of the probability function obtained in Experiment 1A was ratio-dependent. Thus, a primary aim of this experiment was to superimpose the data onto the data from Experiment 1A, in order to determine whether monkeys' representations of numerosity obeyed the superimposition prediction of Weber's Law. In addition, we manipulated the presence or absence of outside values to determine the effect on the psychophysical function.

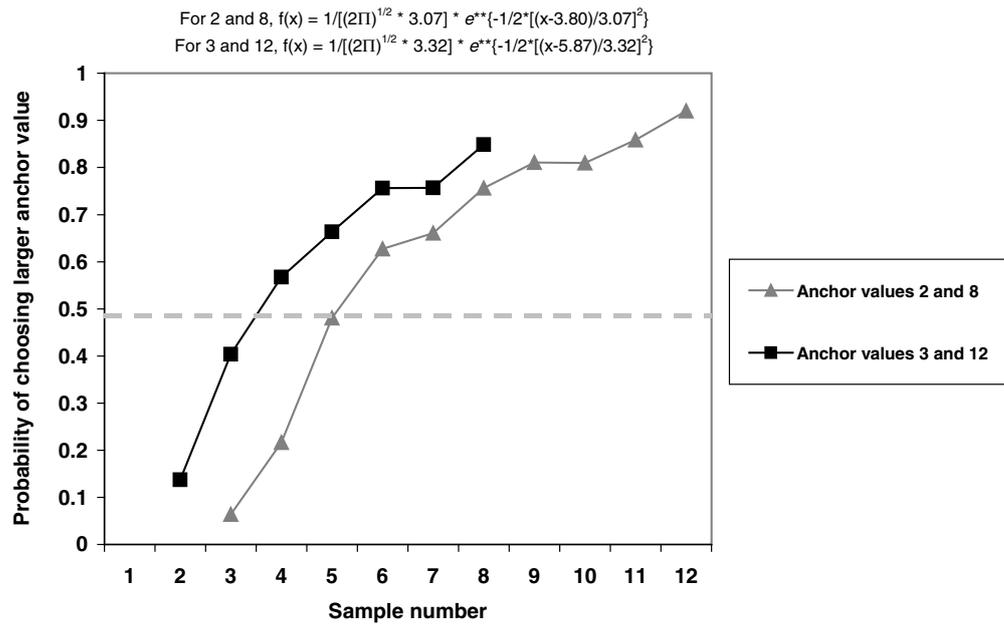
Method

The same three monkeys served as subjects. Monkeys were trained over approximately 500 trials to match novel exemplars of 3 and 12. Subsequently, monkeys were tested with 1800 bisection trials. In these trials, the choice stimuli were the numerosities 3 and 12; however, the samples included all of the values 3–12. As in Experiment 1A, 70% of trials were reinforced (positive or negative) and involved only the sample numerosities 3 and 12. The remaining 30% of trials were unreinforced in that neither juice reward nor time-outs were delivered. Fifty percent of the unreinforced trials presented the numerosities 3 and 12 as samples. On the remaining 50% of unreinforced trials (15% of all trials) the sample was an exemplar of a numerosity equal to or larger than 4 and less than or equal to 11. The stimuli contained 8 exemplars of each numerosity.

To ensure that the monkeys used numerosity as the basis for success in the task, the stimulus parameters of color and cumulative surface area were controlled for as follows: The color of the match and distracter was the same, while the color of the sample was different from this color, making it impossible for the monkey to use color to perform above chance expectations. Secondly, in one half of the trials, the cumulative surface area of the sample matched the cumulative surface area of the 3 in the choice stimuli, while on the other half of the trials, the cumulative surface area of the sample matched the cumulative surface area of the 12 in the choice stimuli.

After monkeys completed the 3–12 bisection condition, two monkeys (S and F) were tested on a final bisection condition in which they were again trained to match the anchor values 3 and 12 over approximately 500 trials. They were then tested with 1800 bisection trials in which the choice stimuli were again the numerosities 3 and 12. However, the samples included not only all intermediate values but also the outside values of 1, 2, 13, and 18. These outside values were chosen based on both the ratio and distance of the

Fig. 5 The probability of choosing the larger anchor value as a function of the numerical value of the sample. Data reflect averages over three monkeys for 1800 trials of two bisection conditions with different trained anchor values. As sample number increased, monkeys chose the larger anchor value as the match. The probability of choosing the larger anchor value by chance was 50%



outside values to anchor values: 2 and 13 were a distance of 1 from each anchor value (as were the outside values 1 and 9 in Experiment 1A), while 1 was the same ratio to anchor value 3 as anchor value 12 was to 18. Seventy percent of trials were reinforced (positive or negative) and involved only the sample numerosities 3 and 12. The remaining 30% of trials were non-differentially reinforced. Fifty percent of the non-differentially reinforced trials presented the numerosities 3 and 12 as samples. On the remaining 50% of non-differentially reinforced trials (15% of all trials) the sample was an exemplar of the numerosity 1, 2, 4–11, 13, or 18.

Results and discussion

Figure 5 shows the data from the first 1800 bisection trials with anchor values 3 and 12 from Experiment 1B alongside the first 1800 bisection trials with anchor values 2 and 8 from Experiment 1A. The data from Experiment 1B were fit with a cumulative normal distribution to determine the point of subjective equality, which was determined by the mean of the fit. A fit with the PSE at 5.87 ± 0.96 accounted for 92.0% of the variance.² Single-sample *t*-tests were used to compare the PSEs observed for each monkey in each of two blocks of trials to the arithmetic and geometric means of the anchor values. Results showed that these PSEs were not significantly different from the geometric mean [$t(5) = 0.07711, p = 0.9415$], but were significantly different from the arithmetic mean [$t(5) = -2.971, p < 0.05$]. The fact that the PSEs in both Experiments 1A and B were not significantly different from the geometric means but differed significantly from the arithmetic means

suggests that the monkeys represented number on a linear scale with a ratio comparison rule or a logarithmic scale with a difference comparison rule. The Weber fraction for these data from Experiment 1B was 0.48 and was calculated by finding the ratio of the difference limen to the PSE.

Bisection data from the second condition in Experiment 1B with anchor values of 3 and 12 and samples that included outside values 1, 2, 13, and 18 were also fit with a cumulative normal distribution to determine the PSE, which was determined by the mean of the fit. A fit with the PSE at 6.75 accounted for 96.5% of the variance when outside values were included. The Weber fraction when the outside values were included was 0.27 and was again calculated by finding the ratio of the difference limen to the PSE. The lower Weber fraction could have resulted from inclusion of the outside values or from increased precision over time with task experience. Figure 6 shows the probability that

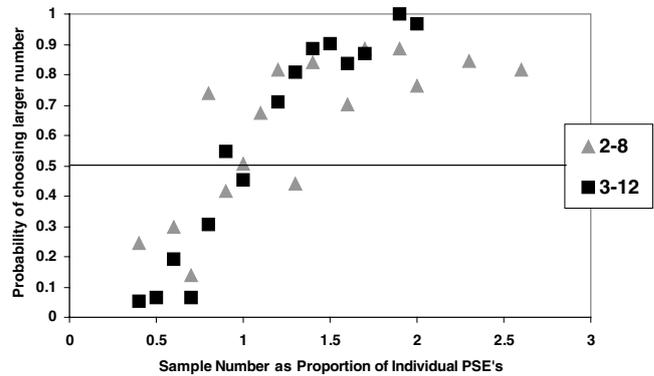


Fig. 6 The probability of choosing the larger anchor value as a function of the sample number (normalized as a proportion of individual PSEs). The plot reflects superimposition of data from the 2 to 8 scale in Experiment 1A and the 3 to 12 scale in Experiment 1B

² As in Experiment 1A, two out of the three monkeys had PSEs near the geometric mean (Monkey M, 5.05; Monkey F, 5.13; Monkey S, 7.96).

the monkeys chose the larger of the two anchor values as a function of the sample number (which is represented as a proportion of individuals' PSEs) with the data for the 2–8 scale and 3–12 scale superimposed to plot along the same relative x -axis. For purposes of comparison, only data that included outside values were included from Experiments 1A and B. The psychophysical curves do not differ significantly [$t(12) = -0.017, p = 0.987$]. The superimposition of the functions confirms the prediction made by Weber's Law and suggests that a single psychological comparison process underlies numerical discriminations independent of the absolute values.

Experiment 2

The bisection task in Experiment 1 demonstrated that monkeys systematically interpolated novel numerical values on an ordinal continuum and that the psychometric functions were ratio-dependent. Here, we sought to determine whether accuracy and latency would be modulated by Weber's Law when monkeys were required to make a more precise numerical match in a DMTS task for which the correct choice was an exact numerical match and the distracter varied in number. Specifically, would accuracy and reaction time be influenced by the ratio of the correct-to-incorrect numerical choice? Although many studies have tested the ordinal numerical abilities of monkeys, comparably fewer have assessed their ability to form a representation of a specific numerical value (cardinal or absolute number judgment).

A secondary question our design allowed us to address was whether the time monkeys take to process the sample stimulus depends on the number of elements in the sample.³ Since the monkeys activated the disappearance of the sample, the amount of time they had to process the sample was under their control. If monkeys serially scan elements in a to-be-enumerated array, their reaction time to touch the sample could be expected to increase with sample numerosity.

Method

Subjects

Two of the three monkeys tested in Experiment 1 were tested, Monkey S and Monkey F.⁴

Apparatus

The apparatus was the same as that used in Experiment 1.

³ Latencies to touch the sample numerosity were not recorded in Experiment 1.

⁴ Monkey M developed motivation problems during Experiment 1, resulting in entire sessions during which she would not participate. These difficulties prevented her from serving as a subject in Experiment 2.

Stimuli

Stimuli included three exemplars for each numerosity. The match and distracter always had the same color, while the sample had a different color; in this way, monkeys could not use color to match the stimuli. In half of the trials, the cumulative surface area of the match was smaller than that of the sample and cumulative surface area of the distracter was larger than that of the sample, while on the other half of the trials, the cumulative surface area of the match was larger than that of the sample and the cumulative surface area of the distracter was smaller than that of the sample. The elements within each stimulus were circles and varied in diameter from .4 cm to 2.4 cm. Elements within a stimulus were uniform in size.

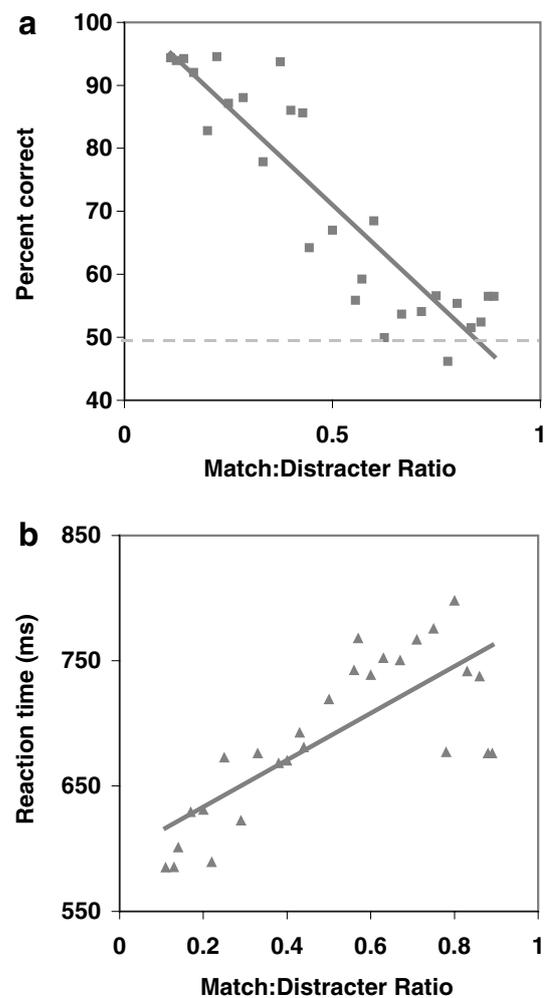
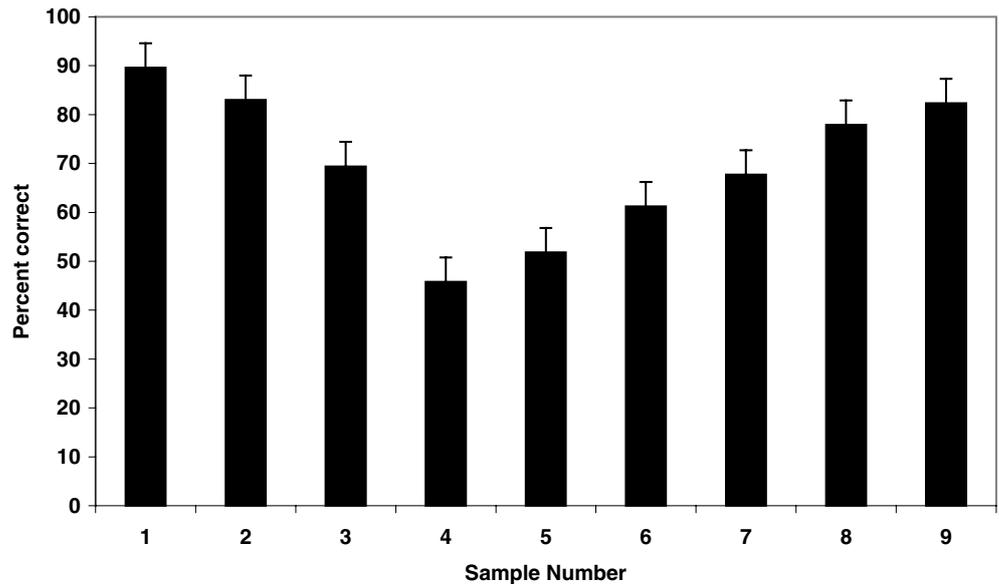


Fig. 7 **a** Accuracy in a DMTS task involving the numerosities 1–9 in Experiment 2. The chance line is graphed at 50%. Accuracy decreases as match:distracter ratio increases. **b** Reaction time for correct responses in a DMTS task involving numerosities 1–9 in Experiment 2. Reaction time increases with match:distracter ratio. All data reflect averages across two monkeys

Fig. 8 Accuracy in a DMTS task testing sample numbers 1–9 in Experiment 2. Accuracy is depicted here as a function of sample number; data reflect averages across two monkeys



Procedure

The same DMTS task was used as in Experiment 1. However, the sample could be any value between 1 and 9, and the choice stimuli contained one exemplar of the sample numerosity and one exemplar of any other numerosity in the range of 1–9. All correct matches were positively reinforced with juice and brief visual and auditory feedback as described for Experiment 1, and all incorrect responses were negatively reinforced with a time-out. Testing occurred for approximately 2400 trials.

Results and discussion

As predicted by Weber's Law, accuracy was found to be a function of the ratio between the correct choice and the distracter. Figure 7a and b show that accuracy decreased as the ratio between the match and distracter approached 1 ($r^2 = 0.83$, $p < 0.05$) and reaction time for correct responses increased as the ratio between the match and distracter approached 1 ($r^2 = 0.59$, $p < 0.05$).

Figure 8 shows accuracy as a function of sample number. Accuracy was highest for the extreme values and lowest for intermediate values. This trend can be explained by Weber's Law. Each of the nine sample numerosities occurred with equal frequency, with each of the remaining eight numerosities serving as distracters. Consequently, the average ratio (small/large) of the sample to distracter exhibited a U-shaped function, with intermediate values having the least favorable average Weber fractions.⁵ Thus, accuracy to the sample was predicted by the average ratio between the sample and distracters. *t*-Tests were used

with all possible combinations of numerosities (each of which occurred at least 30 times; mean values across the two monkeys were used) to test whether monkeys differentiated between these numerosities. We predicted that monkeys' discrimination would show modulation by Weber's Law (for example, they would be more accurate at discriminating small numerosities than at discriminating large numerosities of the same distance). Discrimination scores did not differ significantly for 3 versus 4 [$t(30) = 0.68$, $p = 0.65$], 4 versus 5 [$t(29) = -0.04$, $p = 0.86$], 5 versus 6 [$t(29) = 0.42$, $p = 0.75$], 6 versus 7 [$t(31) = -0.97$, $p = 0.22$], 7 versus 8 [$t(29) = -1.11$, $p = 0.081$], 8 versus 9 [$t(29) = 1.06$, $p = 0.089$], 4 versus 6 [$t(29) = -0.53$, $p = 0.72$], 5 versus 7 [$t(30) = -1.15$, $p = 0.067$], 4 versus 7 [$t(29) = -1.35$, $p = 0.059$], or 7 versus 9 [$t(30) = -1.14$, $p = 0.069$]. All other pairs of numerosities were significantly discriminable.

Although there was a slight improvement in accuracy from the beginning to end of testing, this difference was not significant. Average accuracy for the first three testing blocks of 400 trials for each of the two monkeys was 68.7%, while average accuracy for the last three testing blocks of 400 trials for each of the two monkeys was 70.6% [$t(5) = 0.61$, $p = 0.55$]. Although accuracy may have increased after longer training, the steady-state performance observed over these twelve 400-trial blocks suggests that the monkeys were using a numerical strategy from the outset that was not heavily influenced by reinforcement.

To assess the impact of continuous variables on monkeys' accuracy, we analyzed accuracy as a function of whether cumulative surface area and contour length were congruent or incongruent with number. We also compared monkeys' accuracy in trials for which number was congruent versus incongruent with these continuous variables during the first block of 400 trials versus the last block of 400 trials, to examine the effect of extended training. Results of these analyses are shown in Table 2. A 2 (congruent

⁵ Average Weber fractions for each sample numerosity were as follows: 1, 0.229; 2, 0.395; 3, 0.498; 4, 0.560; 5, 0.591; 6, 0.597; 7, 0.582; 8, 0.549; 9, 0.500.

Table 2 Results of the effects of stimulus congruence and incongruence with number on accuracy in Experiment 2

	SA congruence (%)	SA incongruence (%)	CL congruence (%)	CL incongruence (%)
Overall accuracy	67.90 ± 2.50	71.00 ± 4.30	72.00 ± 7.00	64.50 ± 2.10
1st 400 trials	63.00 ± 1.50	74.00 ± 7.00	74.50 ± 8.20	61.00 ± 1.40
Last 400 trials	71.00 ± 2.80	71.00 ± 1.50	69.50 ± 6.00	68.65 ± 2.30

Note: Continuous variables represented include cumulative surface area (SA) and contour length (CL)

versus incongruent) by 2 (first 400 trials versus last 400 trials) by 2 (continuous variable: Surface area versus contour length) ANOVA showed no main effects or interactions. One-sample *t*-tests analyzing data in blocks of 40 trials showed that accuracy was significantly above chance during both the first 400 trials when each continuous variable was congruent (surface area: $t(9) = 7.96, p < 0.05$; contour length: $t(9) = 15.27, p < 0.05$) or incongruent (surface area: $t(9) = 6.49, p < 0.05$; contour length: $t(9) = 9.04, p < 0.05$) with number, and the last 400 trials when each continuous variable was congruent (surface area: $t(9) = 12.43, p < 0.001$; contour length: $t(9) = 8.99, p < 0.001$) or incongruent (surface area: $t(9) = 9.88, p < 0.001$; contour length: $t(9) = 13.4, p < 0.001$) with number.

The monkeys responded to the sample extremely rapidly with an average of 374.6 ms. Their reaction time to the sample was not dependent on the numerosity of the sample ($r^2 = 0.45, p = 0.23$). As shown in Fig. 9, monkeys were just as fast to extinguish a sample with seven or eight elements as they were to extinguish a sample with two or three elements [$t(5) = 0.88, p = 0.54$]. If monkeys serially enumerated each element in the sample array, we should expect reaction time to increase with the numerosity of the sample. Thus, these data provide no support for the hypothesis that monkeys serially process simultaneous visual arrays in this DMTS task.

General discussion

The main findings of these experiments were that (1) Weber's Law controlled performance of monkeys in both a

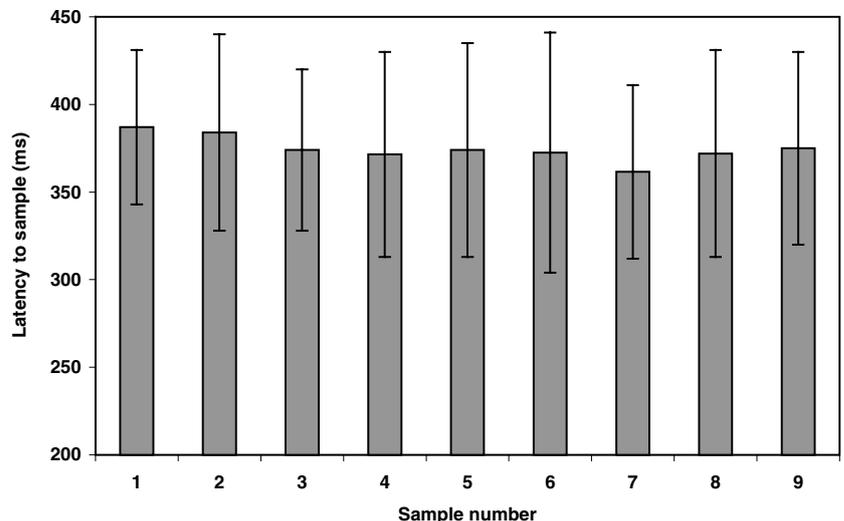
numerical bisection task requiring similarity judgments and a match-to-sample task requiring a precise numerical match, (2) monkeys used purely numerical representations and were not significantly impacted by non-numerical variables, and (3) monkeys were unlikely to have used a serial enumeration process in this type of numerical task. In the following section, we discuss a number of critical issues raised by this research.

Stimulus control by numerosity

Our analysis of the acquisition data from Experiment 1A suggested that monkeys matched stimuli based on numerical equivalence and regardless of other parameters that often co-vary with numerosity. Analyses of accuracy as a function of whether the continuous variables of cumulative surface area, contour length, and density were congruent versus incongruent with number during training showed that the behavior of the monkeys was controlled by numerosity and not other dimensions that often co-vary with numerosity. While monkeys improved their overall accuracy with training (i.e., their accuracies for the last 100 trials of training were always greater than their accuracies for the first 100 trials of training), they improved by similar amounts on congruent versus incongruent trials. Furthermore, even during their first 100 trials, monkeys showed similar accuracies on congruent versus incongruent trials across all continuous variables analyzed.

The design of our study did not investigate the relative salience of continuous variables versus number. Instead,

Fig. 9 Latency to touch the sample numerosity in Experiment 2 DMTS task. Standard errors reflect variability between two monkeys



the design ensured that monkeys could not use continuous variables but could still perform the task with above chance accuracy. The data indicate that monkeys were able to match stimuli based purely on number and did not rely on continuous variables to make their matches. This is consistent with previous ordinal numerical studies. For example, Brannon and Terrace (2000) found that monkeys relied on number rather than continuous variables such as surface area and element size when tested in a numerical ordering task requiring them to learn to order arrays composed of 1, 2, 3, and 4 elements in ascending or descending numerical order and then extrapolate such rules to order the numerosities 5–9 (see also Cantlon and Brannon 2005; Cantlon and Brannon 2006; Judge et al. 2005; Smith et al. 2003).

Evidence for Weber's Law

The probability of choosing the larger anchor value in the bisection experiment increased with the sample number for two different sets of absolute anchor values. This is evidence that, rather than treating novel numerosities as completely discrete, unconnected entities to be categorized randomly, monkeys spontaneously and systematically interpolated novel values along an ordinal numerical continuum. Furthermore, the midpoints or PSEs in the two conditions of the bisection task were not significantly different from the geometric means of the anchor values but were significantly different from the arithmetic means. This suggests that the monkeys represented number on a linear scale with a ratio comparison rule or a logarithmic scale with a difference comparison rule. Our experiment cannot differentiate between these two possibilities, as both types of scaling would predict our results. These data are also consistent with data from studies with rats and pigeons that have shown that the PSE in numerical and temporal bisection tasks is at the geometric mean (e.g., Church and Deluty 1977; Fetterman 1993; Meck and Church 1983; Meck et al. 1985; Platt and Davis 1983; Roberts 2005; Stubbs 1976). These data are in contrast, however, to data from human children and adults tested on a temporal and number bisection task, which show that the PSE was closer to the arithmetic mean (Droit-Volet et al. 2003).

Experiment 2 asked whether the accuracy and speed of monkeys' numerical matches were modulated by ratio, as would be predicted by Weber's Law. We found that monkeys' accuracy indeed decreased as the match-to-distracter ratio increased (Fig. 7a). Furthermore, the monkeys' reaction time for correct responses increased with increases in the match to distracter ratio, perhaps reflecting an increase in animals' threshold of certainty with more difficult ratios (Fig. 7b). These data are consistent with a variety of data using different species and paradigms (e.g., Beran 2004; Beran et al. 2005; Cantlon and Brannon 2006; Judge et al. 2005; Olthof et al. 1997; Smith et al. 2003; Washburn and Rumbaugh 1991). For example, Brannon and Terrace (1998) showed that, for rhesus monkeys that had learned an ordinal numerical rule and were tested with

novel numerosities, accuracy increased as numerical distance between the two test stimuli increased. Nieder et al. (2002) also found that, for rhesus monkeys trained on a numerical same-different task, monkeys' accuracy increased as the numerical distance between the two displays increased. Moyer and Landauer's (1967) classic experiment with adult humans likewise showed that as human subjects were asked to order increasingly distant pairs of Arabic numerals, their accuracies increased; similarly, their latency to respond decreased as the distance between the numerals increased. Taken together, these data are compatible with an analog magnitude nonverbal representation of number governed by Weber's Law and common to adult humans and nonhuman animals.

Effects of learning on numerical discriminations

In Experiment 1A accuracy showed a statistically significant, but small, improvement from the first to the last 100-trial block of training. Despite this improved accuracy over time, each monkey did show above chance performance in training on all stimulus controls even within the first 100 trials. In the bisection task, the shape of the bisection function did not change over time; however, the Weber fractions did decrease over time, indicating an increase in sensitivity to number. In Experiment 2, however, monkeys showed no effect of learning over time; there was no statistical difference in accuracy between the first three testing blocks and the last three testing blocks. Taken together, data from both the experiments suggest that monkeys were able to rapidly use the numerical attribute of the stimuli, and that although reinforcement and experience may have increased precision in the first experiment, there was little benefit to the additional training experienced in Experiment 2.

The influence of outside signals on the PSE

Previous research has led to the suggestion that animals switch decision rules when outside signals are included in bisection tasks. Specifically, it has been argued that animals employ a proximity decision rule rather than the similarity decision rule traditionally thought to underlie temporal bisection without outside signals (Siegel 1986; Siegel and Church 1984). A similarity decision rule entails simultaneously comparing the ratio of the sample numerosity to each trained anchor to decide whether the sample is closer to the smaller or larger trained anchor value. Thus, animals would compare on every trial (a) the ratio of the sample to the smaller anchor numerosity, against (b) the ratio of the larger anchor numerosity to the sample numerosity. If the ratio between (b) to (a) were greater than 1, the animal would classify the sample numerosity as the smaller anchor value, but if the ratio were less than 1, the animal would classify the sample numerosity as the larger value. If the ratio were equal to 1—by definition, the point of subjective equality—the animal would be equally likely to classify the sample as either anchor value; this occurs at

the geometric mean. This model predicts that the psychometric functions showing the probability of choosing the larger anchor value against sample numerosity should exhibit no difference when outside signals are present versus when they are not; in both situations, the point of subjective equality should be at the geometric mean of the trained anchor values. An additional prediction is that outside signals should be classified as the anchor value to which they are closest. As the obtained PSEs in Experiments 1A and the condition in Experiment 1B lacking outside signals were not significantly different from the geometric means, a model based on use of the similarity decision rule could potentially account for these data.

In contrast to the similarity decision rule, a proximity decision rule would entail determining whether the sample numerosity were close enough to either reinforced anchor value (again through a ratio comparison) to even merit a response. To decide whether values are close enough to trained values to merit a response, it has been postulated that animals using the proximity rule in temporal generalization tasks base such a decision on a discrimination ratio of the absolute difference between actual duration of the probe signal and remembered duration of the reinforced signal, to remembered duration of the reinforced signal (which shows scalar variance); subjects decide a response is warranted if this discrimination ratio is below a threshold (which also exhibits scalar variability; Church and Gibbon 1982). Thus, outside signals that do not exceed a threshold level of proximity to either anchor value should be categorized randomly. Also in contrast to the similarity decision rule, which predicts a similar psychometric function with a PSE at the geometric mean regardless of the presence or absence of outside signals, the proximity decision rule predicts that the addition of outside signals should cause increased precision in numerical discrimination (Siegel 1986). Our data from Experiment 1B may be compatible with this prediction, as the Weber fractions decreased across conditions after outside signals were introduced. This sharper discrimination is postulated to occur in the presence of outside signals because bisection tasks with outside signals have nonreinforced stimuli appearing on both sides of the reinforced anchor values, whereas bisection tasks without outside signals have nonreinforced signals appearing on only one side of the reinforced anchor values; previous results from temporal generalization tasks with pigeons resulted in steeper generalization gradients when nonreinforced stimuli were presented on both sides of the reinforced stimuli (Hanson 1961). Using a proximity decision rule coupled with this increase in discrimination ability when outside signals are present, animals will encounter more instances in which they do not consider the sample close enough to either trained anchor value to warrant a response than they encounter when outside signals are not present. When they do find that the signal is close enough to both the anchor values to warrant a response, they will resort to the similarity rule to resolve this conflict. When outside signals are present, then, animals should use the similarity rule less often; the PSE would thus be less than the geometric mean. Data from temporal bisection tasks that included outside

signals are consistent with this particular prediction of the proximity rule concerning the PSE. For example, in a temporal bisection task with rats when outside signals were included at test, the bisection point fell below the geometric mean of the anchor values (Siegel 1986; Siegel and Church 1984; however, see Meck 1997).

Additional testing with outside signals will be necessary to conclusively determine the effects on the PSE in numerical bisection tasks and whether outside signals affect number processing in the same way as time processing. More parametric analyses of conditions with manipulations other than the inclusion of outside values that have been shown to affect the PSE in temporal bisection tasks with humans—such as using a very large ratio between anchor values or signals with irregular spacing—may also prove informative in this regard (Allan 2002).

Serial versus parallel processing

It has been suggested that animals may use a nonverbal counting process to form numerical representations (e.g., Gallistel and Gelman 1992; Meck and Church 1983). Counting is a serial process that follows three critical principles (Gelman and Gallistel 1978). The one-to-one principle states that there is a one-to-one correspondence between the number of labels applied and the number of to-be-counted elements in a set (labels can be nonverbal). The stable order principle states that the labels are applied in a stable order across counting episodes (I cannot count 1–2–3 today and 3–1–2 tomorrow). The cardinal principle states that the last label applied serves to represent the cardinal value of the set. When elements within a set are presented serially (e.g., sequences of light flashes or tones), animals must process them serially. However, when stimuli are presented as simultaneous visual arrays, it is less clear whether the enumeration process is serial. It is possible that organisms could serially allocate attention to each element in an array, and thus convert a simultaneous array into a sequential array.

It has been argued that rather than using a serial counting process, adult humans use a rapid parallel process to apprehend the value of small numerosities (e.g., Kaufman et al. 1949; Mandler and Shebo 1982; Trick and Pylyshyn 1994). The values used in our tasks exceed the values that are thought to be within the subitizing range. However, alternative parallel enumeration processes have been proposed that can handle larger values (e.g., Barth et al. 2003; Dehaene and Changeux 1993).

Based on behavioral and neurobiological evidence, Nieder and colleagues argued that rhesus macaques use a parallel process to form numerical representations. They found that neurons in prefrontal and parietal cortex in the macaque monkey that were selective for 1, 2, 3, 4, or 5 elements had similar response latencies of approximately 120 ms (Nieder et al. 2002). In addition, they found that the number of visual saccades made by monkeys did not increase with the number of display items in a numerical

same-different task as set size increased from 1 to 7 (Nieder and Miller 2004).

Analyses of reaction time to respond to the sample numerosity in Experiment 2 provided no evidence that monkeys serially enumerate elements when forming numerical representations. Specifically, reaction time did not increase with sample numerosity, as would be expected if monkeys required more time to enumerate larger values. Because we found no increase in reaction time to the sample with increasing sample numerosity, our data support the position that monkeys use a parallel process to form numerical representations in these DMTS tasks.

Conclusion

To sum up, these experiments add to the growing body of data demonstrating that monkeys can represent number independently of non-numerical stimulus dimensions and can interpolate novel values systematically along an ordinal continuum. Furthermore, the superimposition of psychometric functions from two numerical bisection conditions—which used anchors differing in absolute value but equal in ratio—suggests that Weber’s Law applies to cardinal as well as ordinal number judgments in monkeys. In support of this conclusion, both accuracy and reaction time in making absolute numerical matches were modulated by the ratio between the correct choice and the distracter. Finally, there was no evidence that monkeys used a serial enumeration process to form numerical representations of the simultaneous visual arrays with which they were presented. A great deal of research is still necessary to pinpoint the nature of the nonverbal enumeration process, the format of number representations, and the subjective scaling of the mental number line. Answering such questions in a monkey model should provide substantial insight into human numerical cognition.

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