Monkeys (*Macaca mulatta* and *Cebus apella*) Track, Enumerate, and Compare Multiple Sets of Moving Items

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Despite many demonstrations of numerical competence in nonhuman animals, little is known about how well animals enumerate moving stimuli. In this series of experiments, rhesus monkeys (*Macaca mulatta*) and capuchin monkeys (*Cebus apella*) performed computerized tasks in which they had to enumerate sets of stimuli. In Experiment 1, rhesus monkeys compared two sets of moving stimuli. Experiment 2 required comparisons of a moving set and a static set. Experiment 3 included human participants and capuchin monkeys to assess all 3 species' performance and to determine whether responding was to the numerical properties of the stimulus sets rather than to some other stimulus property such as cumulative area. Experiment 4 required both monkey species to enumerate subsets of each moving array. In all experiments, monkeys performed above chance levels, and their responses were controlled by the number of items in the arrays as opposed to nonnumerical stimulus dimensions. Rhesus monkeys performed comparably to adult humans when directly compared although capuchin performance was lower.

Keywords: enumeration, monkeys, *Macaca mulatta*, *Cebus apella*, numerical processing

The quantification skills of nonhuman animals are now well established. These skills include counting-like abilities (e.g., Beran & Rumbaugh, 2001; Boysen & Berntson, 1989; Boysen, Berntson, Shreyer, & Hannan, 1995; Capaldi & Miller, 1988; Matsuzawa, 1985; Pepperberg, 1994, 2006; Roberts, Roberts, & Kit, 2002; Tomonaga & Matsuzawa, 2002), sensitivity to arithmetic manipulations (Beran, 2001, 2004; Beran & Beran, 2004; Boysen & Berntson, 1989; Call, 2000; Flombaum, Junge, & Hauser, 2005; Hauser, Carey, & Hauser, 2000; Sulkowski & Hauser, 2001), and widespread phylogenetic abilities for relative numerousness judgments (e.g., Anderson et al., 2005; Beran, 2007a, 2007b; Boysen & Berntson, 1995; Boysen, Mukobi, & Berntson, 1999; Brannon, Cantlon, & Terrace, 2006; Brannon & Terrace, 2000; Cantlon & Brannon, 2006; Emmerton, 1998; Emmerton, Lohmann, & Niemann, 1997; Jaakkola et al., 2005; Judge, Evans, & Vyas, 2005; Kilian, Yaman, von Fersen, & Gunturkun, 2003; Pepperberg, 2006; Roberts & Mitchell, 1994; Santos, Barnes, & Mahajan, 2005; Thomas & Chase, 1980; Uller, Jaeger, Guidry, & Martin, 2003). Some of these quantity judgments are made on the basis of the number of items in sets resulting from careful controls over the nonnumerical properties of stimulus sets that are used (e.g., Beran, 2007a; Brannon & Terrace, 2000; Jordan & Brannon, 2006). Thus,

number plays an important (although not always dominant) role in the behavior of animals.

A diverse range of perceptual processes can be utilized to make quantity judgments. In addition to assessing the visual quantity of stimuli, we also know that animals are sensitive to auditory quantity (e.g., Davis & Albert, 1986; Hauser, Dehaene, Dehaene-Lambertz, & Patalano, 2002; Jordan, Brannon, Logothetis, & Ghazanfar, 2005), and tactile quantity (e.g., Davis, Mackenzie, & Morrison, 1989). Some species can make quantity assessments across sensory modalities (e.g., Jordan et al., 2005; Pepperberg, 2006).

What might be the reason that number plays an important role in the decision processes of animals? Sensitivity to number certainly affords an animal with greater opportunities for maximizing intake through foraging. Numerical sensitivity also may play a critical role in assessing group strength. For example, lions, monkeys, and chimpanzees may use the number of calls they hear from a competing group to assess the strength of that group (Kitchen, 2004; McComb, Packer, & Pusey, 2004; Wilson, Hauser, & Wrangham, 2001). Sensitivity to number also may be important for keeping track of the members of a group to which one belongs or in keeping track of moving items such as competitors, predators, or prey. This possible benefit of numerical sensitivity provides a new challenge to researchers assessing the nature of numerical cognition in nonhuman animals. Assessing group strength and keeping track of group members would require closely monitoring movement of individuals. This can be critically important in preventing over- or underestimates of the number of individuals in groups. However, little experimental research has examined the relation between item tracking and quantity estimation or enumeration.

In this study, I presented rhesus monkeys (*Macaca mulatta*), capuchin monkeys (*Cebus apella*), and adult humans (*Homo sapiens*) with a variety of quantity discrimination tasks in which sets of items constantly moved on a computer screen. Controls were

included that required use of the number of items rather than the total area of those items or the complexity of movement within the array for correct completion of trials. Sets ranged from 1 to 12 items across the experiments, and movement varied in direction and speed for each item within each set. In this way, participants had to enumerate elements within sets while taking into account individual item movement.

Performance was compared across species as well as across set sizes and set manipulations. These data could be compared to previous studies using static visual sets and sequentially presented sets (in which there was item movement, but of a much less complicated form) to assess the relative difficulty of tracking and enumerating stimulus sets in a comparison task. Manipulations in this study also allowed an assessment of the difficulty of comparing two sets of moving items to comparisons involving one moving set and one static set, and comparisons involving the assessment of subsets of items within two larger moving sets. Finally, one experiment directly compared the performance of monkeys to the performance of adult humans. The data indicate how well nonhuman animals can monitor moving items so as to produce reliable numerical estimations of multiple sets and compare those estimations.

Experiment 1

Method

Participants. Six male rhesus monkeys were tested: Obi (2-years-old), Han (3-years-old), Lou (14-years-old), Gale (24-years-old), Hank (24-years-old), and Willie (22-years-old). All six animals had been trained to respond to computer-generated stimuli, and many had participated in previous numerical tasks (e.g., Beran, 2007a, 2007b; Harris & Washburn, 2005), although none of these involved tracking and enumerating multiple sets of moving items on the computer screen.

Apparatus. Trials were presented on a Compaq DeskPro with an attached 17-inch color monitor. Joystick responses were made with a Gravis GamePad Pro digital joystick mounted vertically to the cage. The test program was written in Visual Basic for Windows. Correctly completed trials were automatically rewarded by the computer with single 94 mg Bio-Serv food pellets through use of an automated pellet dispenser. Details of this testing system are reported elsewhere (Richardson et al., 1990; Rumbaugh et al., 1989; Washburn & Rumbaugh, 1991).

Design and procedure. All animals were tested individually while physically (but not visually) isolated from all other animals in their living quarters. The monkeys had continuous access to the computer program for blocks of time from 4 hours to 12 hours in length, and the computer apparatus was attached to the home cage of each animal at all times. Monkeys chose when to work and when to rest, and they were not deprived of water or regular feedings at any point during the study. Thus, the number of trials completed in a session was determined solely by each monkey. However, the program stopped automatically when the desired number of trials had been completed.

Monkeys manipulated a joystick with their hand to move a cursor on the computer screen, and they initiated each trial by moving the cursor into contact with a rectangle in the center of the screen. The cursor and the rectangle then disappeared and two

outlined boxes (59.5 mm × 63.75 mm) appeared to the immediate left and right of center-screen. Drawn inside those two boxes were different quantities of black dots, ranging in number from 1 to 10, with set sizes randomly selected on each trial with the exception that both sets could not have the same number of items. Each dot was drawn with a diameter of 3 to 12 mm, randomly determined by the program. This helped to partially dissociate amount and number cues for each set, although this dissociation was not complete (see Experiment 3 for trials in which amount and number were dissociated as valid cues). Each dot also was given an initial, randomly selected trajectory and began moving on the screen as soon as it appeared. This movement took place at 1 of 4 randomly selected speeds, and a given dot moved in a straight line until it came into contact with one of the walls of the rectangular outline, at which point it was redirected, appearing as if it had deflected off the wall. Each dot, however, started by moving in a randomly determined direction, so the movement appeared chaotic on the screen. All dots in both sets appeared at once and were moving immediately. When dots approached each other, their movement created the illusion that they passed through (or over/under) each other (in other words, they did not bounce off each other). Therefore, the monkeys saw two immediately visible, randomly moving sets of stimuli. After the dots appeared, there was a 1,500 ms delay before the cursor appeared directly between the two rectangles and could be moved by the monkey into contact with one of those rectangles. This constituted the selection by the monkey and ended a trial. Dot movement continued throughout the entire trial, and the stimuli remained on the screen until a monkey made a response. There was no time limit to how fast the monkeys had to respond.

If the selected set contained the larger number of dots, the monkey was given a melodic tone as feedback and received a single food pellet. If the selection was incorrect, a buzz sounded and a 10-s timeout was presented during which the screen remained blank. The intertrial interval was 1 second, followed by the beginning of the next trial. Each monkey completed 1,000 trials in this experiment.

Results

Overall, the monkeys performed at very high levels, indicating that this was not a difficult task for them. They also learned the task rule almost immediately, as all animals were correct on 90 or more trials in the first block of 100. Thus, there was little need for experience with the task to discern the rule for responding, although it was very likely that previous experimental studies (e.g., Beran, 2007a, 2007b; Harris, Washburn, Beran, & Sevcik, 2007) had taught the monkeys that quantity was an important cue in new tasks.

Performance is presented in Figure 1A as the mean percentage of trials correct as a function of the quantitative difference between the two sets. There was a significant positive correlation of difference and mean percentage of trials correct, $r(7) = .79, p < .01$, and this indicated that mean performance of the monkeys increased as the quantitative difference increased. Figure 1B presents performance as a function of the ratio of smaller set size to larger set size. Here, there was a significant negative correlation, $r(29) = -.85, p < .01$, and this indicated that mean performance decreased as the ratio increased. These measures consistently account for performance in numerousness judgment tasks (e.g., Beran, 2001,
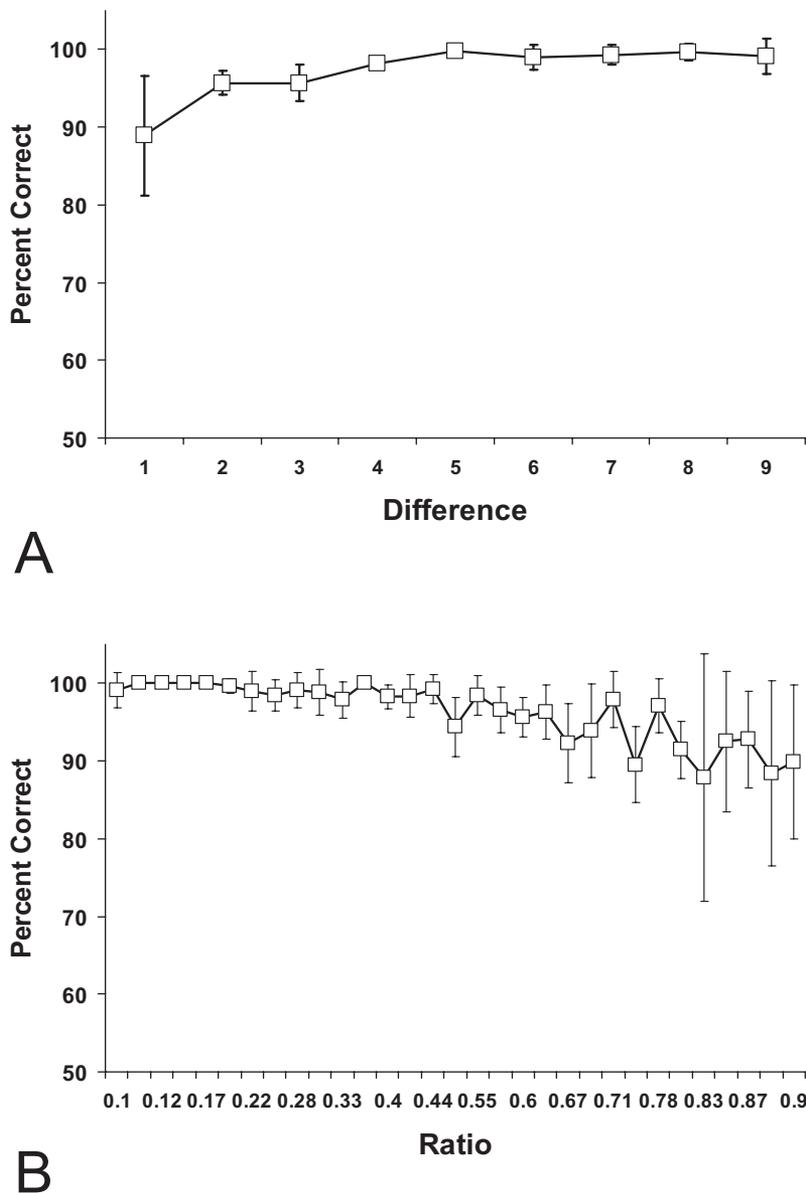
Figure 1. Mean performance at each difference (A) and each ratio (B) in Experiment 1. Bars indicate 95% confidence intervals. Note that the *y*-axis starts at 50%, which is the chance level of performance.

2004; Brannon & Terrace, 2000) as they reflect the magnitude and distance effects. A Repeated Measures Analysis of Variance with ratio as the independent variable and performance as the dependent variable indicated that there was a strong effect of the ratio on performance, $F(30, 150) = 4.24$, $p < .01$, $\eta_p^2 = .46$.

Discussion

Enumerating moving stimuli was not difficult for this sample of monkeys. Despite the fact that items were never stationary, the monkeys apprehended the larger set and selected that set at very high levels of performance. As in many past studies, the ratio and the difference between sets were highly correlated with performance across this range of set quantities. Despite

this high performance, however, there was no reason to assume that the number of dots in the two sets controlled responding. Even though individual dot sizes were varied, there were no systematic data that differentiated between trials in which the numerically larger set also contained the greater mass or amount of dots compared to trials where those two cues were not confounded. This will be the focus of Experiment 3. However, another potential cue that the monkeys may have used was a perceptual summation of the extent to which arrays were chaotic because of the movement of their elements. The addition of more items to a set necessarily increased the amount of movement in that set and the complexity of the resulting visual appearance of the array. This, too, would be a non-numerical

and nonquantitative cue. Experiment 2 examined whether monkeys were responding to this cue.

Experiment 2

Experiment 1 may have afforded a cue to the correct response based on the level of chaotic movement perceived in each set. In other words, the monkeys may have responded to how much movement was present within each of the sets. This cue would be evident even with the differing sizes and speeds of the moving items. Therefore, in Experiment 2 only one set of stimuli moved on the screen whereas the second set remained stationary throughout the trial. In approximately half of the trials, the smaller set remained stationary, and in the other half, the larger set remained stationary. Thus, the monkeys could not respond to these trials solely based on some form of summation of the amount of movement or complexity of the stimulus array because such cues were not available for both sets.

Method

Participants and apparatus. One monkey (Gale) did not participate in this experiment for reasons not related to the study. A new monkey (Luke, 6-years-old) was added, and he had a comparable testing history to the other monkeys. The apparatus was identical to Experiment 1.

Design and procedure. The design was very similar to Experiment 1. The only modification was that one of the two sets (randomly determined by screen side on each trial) was presented as a static array. In the static set, dots were assigned to random locations within the set exactly as in Experiment 1 except that they did not move. All other details were the same as in Experiment 1, and all monkeys again completed 1,000 trials.

Results

Performance is presented in Figure 2 again as a function of the difference (A) and the ratio (B) between sets. There was a significant positive correlation of difference and mean percentage of trials correct, $r(7) = .89, p < .01$. There was a significant negative correlation of ratio and mean percentage of trials correct, $r(29) = -.92, p < .01$. A Repeated Measures Analysis of Variance with ratio as the independent variable and performance as the dependent variable again indicated that there was a strong effect of the ratio on performance, $F(30, 150) = 4.22, p < .01, \eta_p^2 = .46$. Additionally, there was no difference in performance between trials in which the moving set was the larger set and trials in which the static set was the larger set, $F(1, 5) = 1.81, p = .24, \eta_p^2 = .26$.

Discussion

Rhesus monkeys quickly learned to select between one static set and one moving set of stimuli using a quantitative judgment cue. This performance was not supported through responsiveness to the amount of chaos or movement in each array as these dimensions were eliminated in the static set (which still was the correct choice on half of the trials). However, it remained to be demonstrated that number was the dominant stimulus cue used by the monkeys in this task. To show that number was relevant in the monkeys' judgments, it was necessary to have a condition in which number

of dots and amount or mass of the dots were not confounded. Otherwise, the monkeys may have been responding simply to the relative sizes of the two arrays in terms of the mass of dot material presented in each array. However, if performance still exceeded chance levels when these two stimulus dimensions sometimes offered conflicting cues, this would indicate that the monkeys were responding to the number of items in the two sets. This would also indicate that number is a salient dimension of moving stimuli for these monkeys.

Experiment 3

Two new species were added to this experiment. Given the success of the rhesus monkeys in Experiment 1 and Experiment 2, and previous reports that capuchin monkeys also succeed at some numerical cognition tasks (e.g., Beran, 2008; Judge et al., 2005), capuchin monkeys were included in this study to provide a more comparative assessment of tracking and enumerating skills of monkeys. In addition, adult humans were tested to expand the comparative assessment of this type of quantification skill by allowing a direct comparison of human performance and monkey performance.

Method

Participants and apparatus. All seven previously tested rhesus monkeys were included in this experiment. Seven capuchin monkeys (*Ceubs apella*) also were tested: Logan (male, 2-years-old), Liam (male, 3-years-old), Wren (female, 4-years-old), Nala (female, 4-years-old), Gabe (male, 9-years-old), Griffin (male, 9-years-old), and Drella (male, 16-years-old). All capuchins previously had been trained to respond to computer-generated stimuli in the same way as the rhesus monkeys, and they worked on the computer task used in this experiment for 1.5 to 2 hours each day. The capuchins previously had been trained to sequence Arabic numeral stimuli (Beran et al., in press) and make judgments between two stationary sets of discrete stimuli that were presented in various arrangements (Beran, 2008), but they had no experience with tracking and enumerating moving stimuli.

Ten human participants (mean age, 19.7 years; 6 females, 4 males) were recruited from Georgia State University and were given course credit for participation.

The apparatus was identical to the previous experiments for the monkeys. Humans also responded through use of identical joystick responses, although joysticks were held by human participants in their hands so that the orientation of the joystick was more variable to meet the comfort level of the participant.

Design and procedure. The design was identical to Experiment 1 with one exception. There was no longer any delay between the appearance of the sets and the appearance of the joystick that allowed participants to make a response. Dot movement continued throughout the entire trial, and the stimuli remained on the screen until a participant made a response. The major change between Experiment 1 and this experiment pertained to the data that were stored by the computer program. The program now recorded the total amount of pixilation from all of the dots in a given set so that the two sets could be related to each other based on their levels of pixilation. Thus, trials could be sorted by the number of items in each set and also by the amount of illumination from each set.
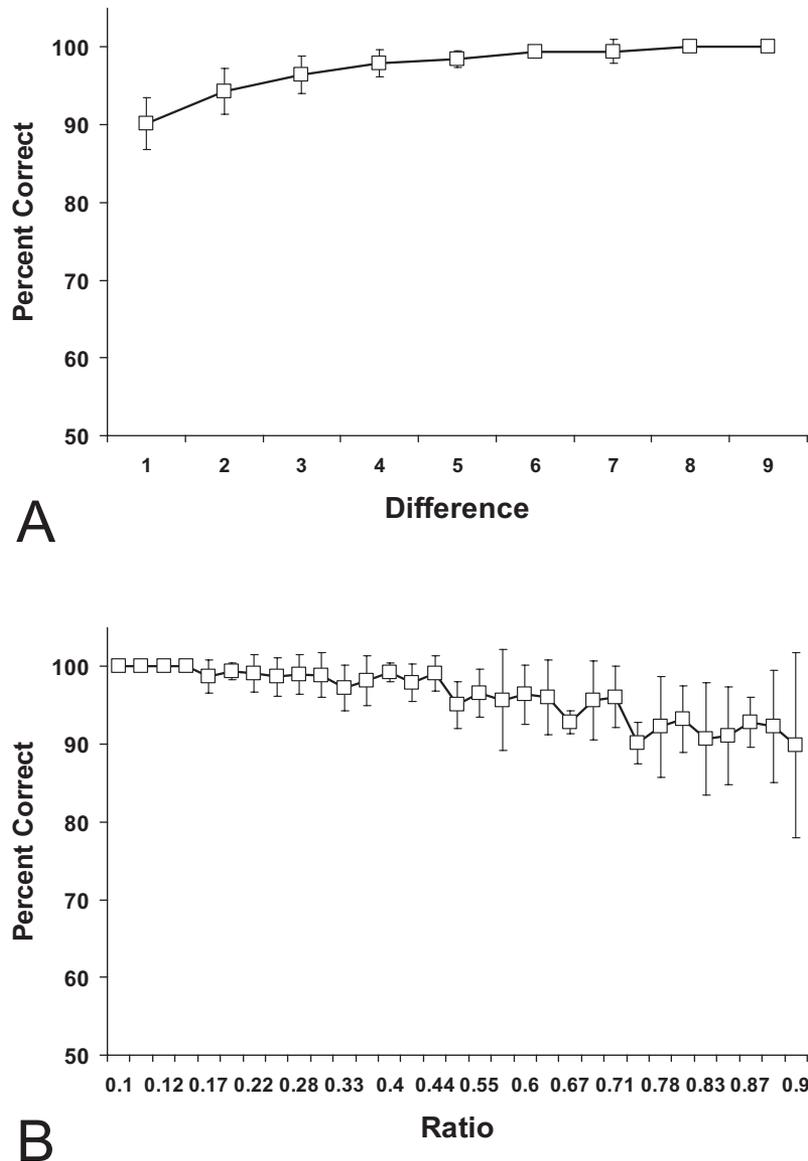
Figure 2. Mean performance at each difference (A) and each ratio (B) in Experiment 2. Bars indicate 95% confidence intervals. Note that the *y*-axis starts at 50%, which is the chance level of performance.

Human participants were given limited verbal instructions about the task. Specifically, they read the following statement on the screen at the start of the experiment:

"Please use the joystick in front of you to move the cursor (the red dot below) on the screen. Start each trial by touching the rectangle in the center of the screen. Then, you will see two sets of dots. For the first part of the experiment, after you pick one set you will be told if your choice was correct or not, and you should try to learn the simple rule for making choices. Throughout the experiment, the number of trials remaining is shown in the top left corner. Please try to get as many trials correct as you can using the simple rule that you will learn at the beginning. Press the space bar to begin the experiment, and then make all remaining responses with the joystick."

All monkeys again completed 1,000 trials, and human participants each completed 300 trials. Neither species was given a time limit for making a response.

Results

Performance is presented in Figure 3 again as a function of the difference (A) and the ratio (B) between sets. Performance was significantly different as a function of the species, $F(2, 21) = 14.66$, $p < .001$, $\eta_p^2 = .58$. Post hoc analyses (Tukey's HSD) indicated the human performance and rhesus monkey performance were significantly higher than capuchin performance, $p < .05$, but human performance and rhesus monkey performance did not differ from each other.
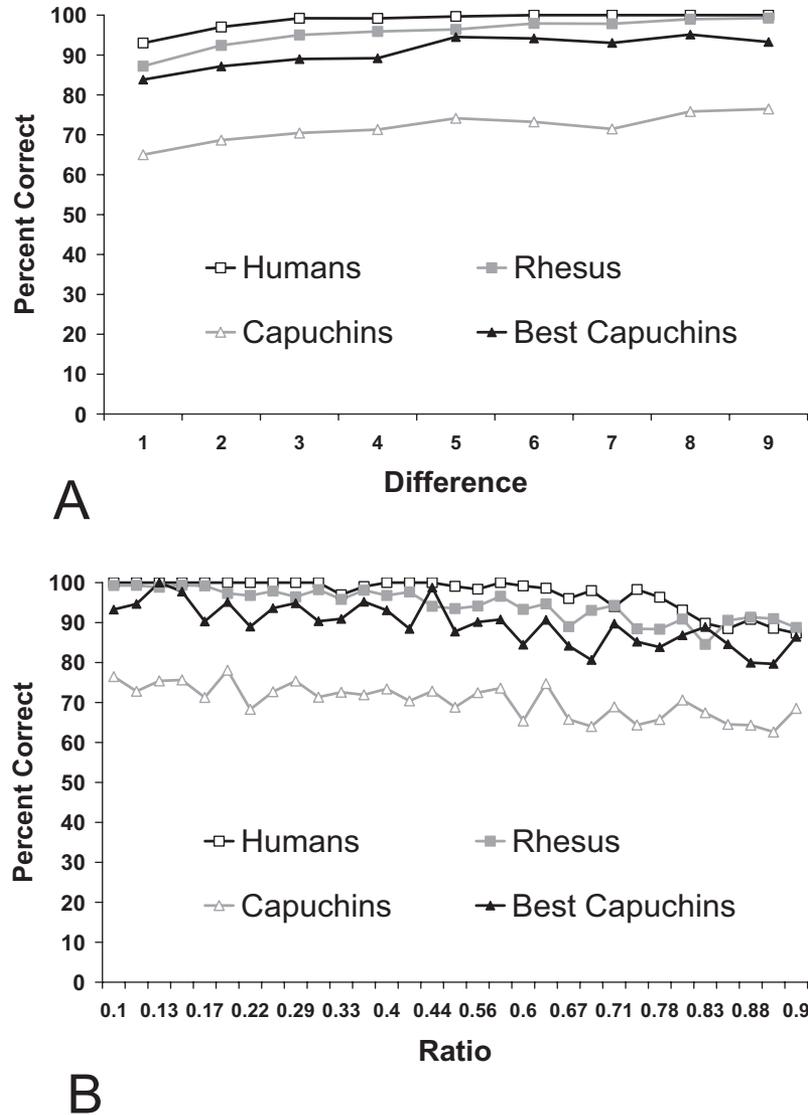
Figure 3. Mean performance for each species at each difference (A) and each ratio (B) in Experiment 3. Separate data are shown for the three best performing capuchin monkeys.

Rhesus monkeys and humans performed at very high levels. For the rhesus monkeys, there was again an effect of the ratio between sets on performance, $F(30, 216) = 3.37$, $p < .01$, and there was a significant negative correlation between the ratio and mean performance, $r(29) = -.89$. There was a significant positive correlation of difference and mean percentage of trials correct, $r(61) = .65$, $p < .001$. Human participants also demonstrated an effect of the ratio between sets on performance, $F(30, 309) = 3.02$, $p < .01$, and there was a significant negative correlation between ratio and mean performance, $r(29) = -.80$. There was a significant positive correlation of difference and mean percentage of trials correct, $r(88) = .53$, $p < .001$.

For capuchins, there was not an effect of the ratio between sets on performance, $F(30, 216) < 1.0$, $p > .05$. There also was not a significant positive correlation of difference and mean percentage of trials correct, $r(61) = .16$, $p = .22$. However, an examination of

individual performances revealed that 3 of the 7 capuchin monkeys performed at very high levels overall (and more comparable to the performance of the macaques; see Figure 3). Those monkeys, Liam, Logan, and Wren, demonstrated a significant negative correlation between ratio and mean performance, $r(29) = -.78$, and the effect of the ratio on performance approached statistical significance, $F(30, 92) = 1.55$, $p = .07$.

Because of the differences in performance across capuchin monkeys, I examined performance on the first 100 trials and the last 100 trials to determine whether any of those monkeys showed improved performance with experience. Five of the seven animals did ($p < .05$ as assessed with χ^2 tests of independence). Therefore, the majority of the capuchin monkeys improved with experience on this task.

An additional analysis was conducted for each monkey species. This analysis compared performance on those trials in which the

numerically larger set had the smaller amount or area in terms of pixel illumination on the screen (the *incongruent* condition) compared to trials in which number and amount/area were confounded (the *congruent* condition). Because of the small number of trials for some ratios, all trials were sorted into 1 of 9 bins based on the ratio between sets (ranging from ratios of .10 to .90). Rhesus monkeys (Figure 4A) performed slightly better overall on trials in the incongruent condition, but this difference was not statistically significant, $t(6) = 2.06$, $p = .08$. Capuchins (Figure 4B) showed no difference in performance between the two trial types, $t(6) = 1.76$, $p = .13$.

The response time data for all three species are presented in Figure 5. All trials with response times greater than 10 seconds were excluded from the analysis (these constituted less than 1% of the trials), and analyses only included trials that were completed correctly. A repeated measures ANOVA with ratio as a within subjects factor and species as a between subject factor indicated a significant main effect of ratio, $F(30, 630) = 8.06$, $p < .001$, but there was not a main effect of species, $F(1, 21) = 2.95$, $p = .074$. There was a significant interaction between those two variables, however, $F(60, 630) = 5.68$, $p < .001$. All three species produced data that were best fit with a cubic function, suggesting relatively shallow increases in response time when the ratio between sets was small with a steeper increase across the range of larger ratios. Although this function was much more pronounced for the human data, the function
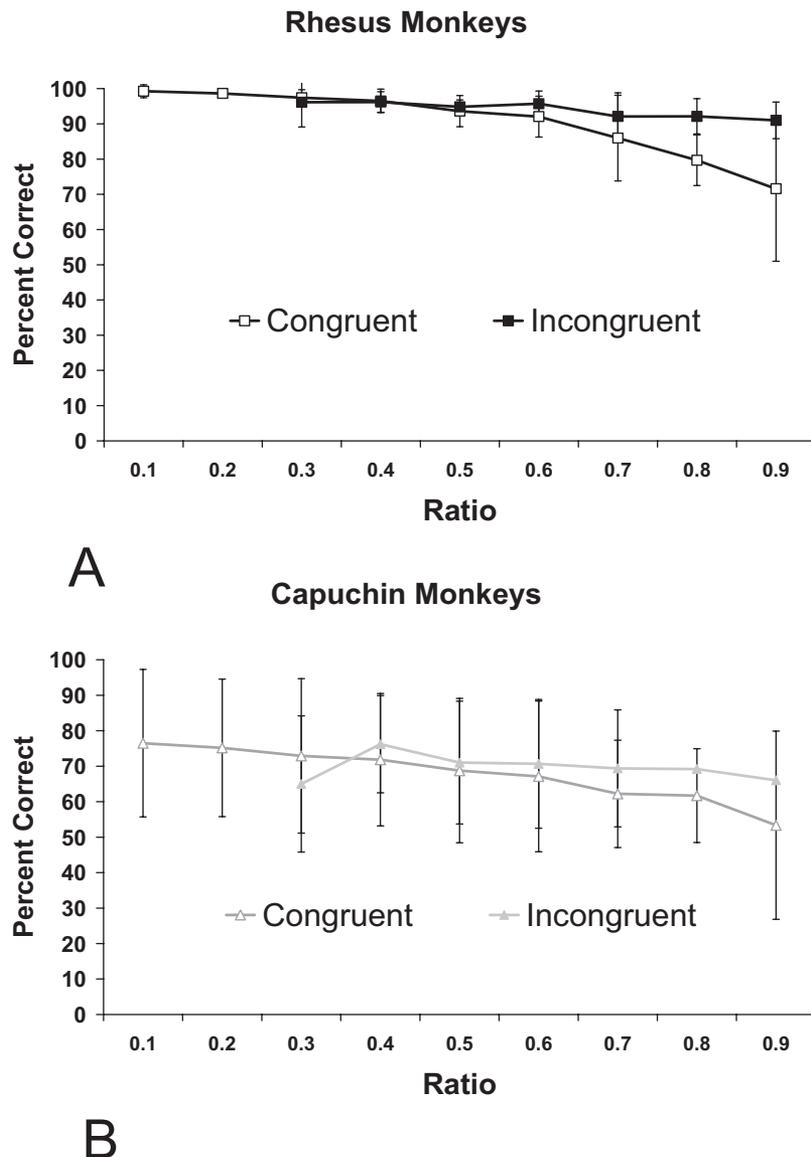

Figure 4. Mean performance at each ratio in Experiment 3 for rhesus monkeys (A) and capuchin monkeys (B). Data are shown for two conditions. The congruent condition involved equally valid numerical and amount cues (see text) whereas the incongruent condition did not. Bars indicate 95% confidence intervals.
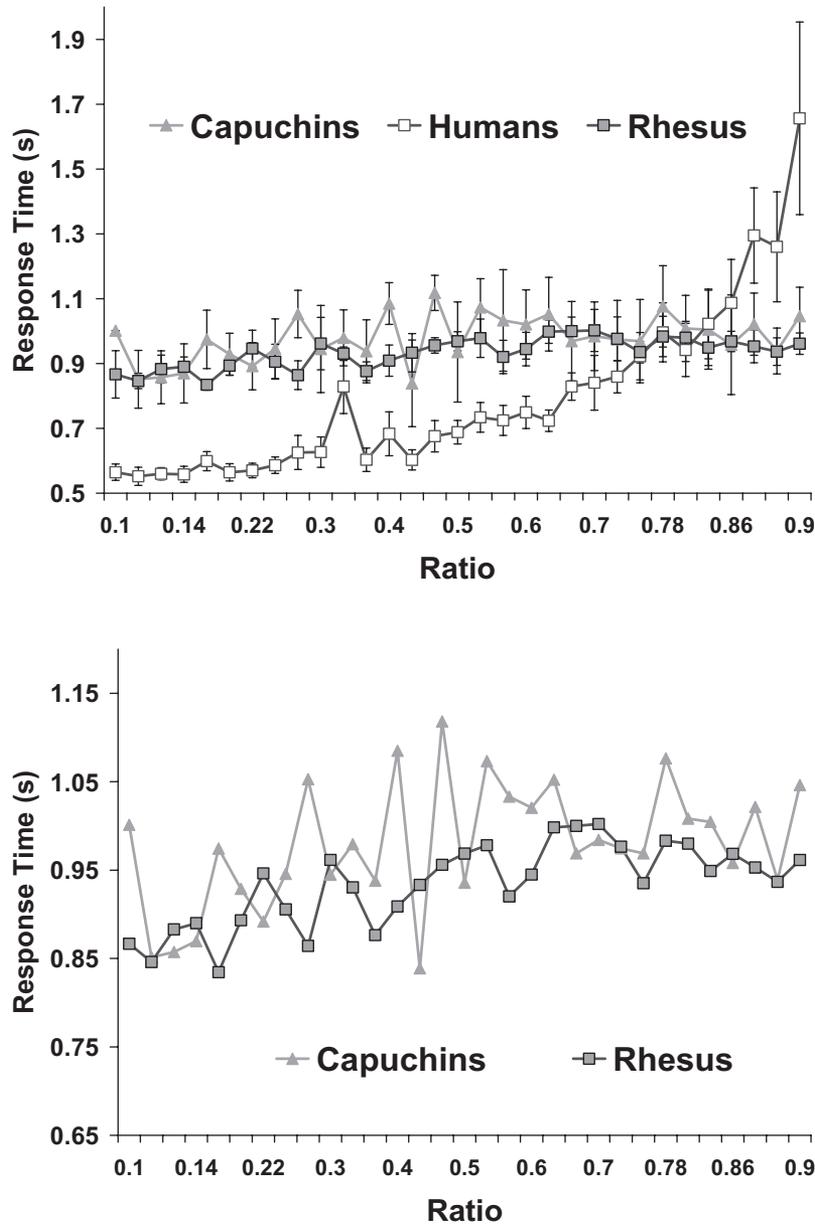
Figure 5. Mean response times as a function of the ratio between sets for all three species. Bars indicate standard errors of means. Because of the more restricted temporal range for monkey responses, those data are replotted in the lower graph to show the relation between response time and ratio.

was statistically significant for all species, rhesus: $F(3, 27) = 17.57$, $p < .001$, $R^2 = .67$; capuchins: $F(3, 27) = 3.47$, $p = .03$, $R^2 = .27$; humans: $F(3, 27) = 93.19$, $p < .001$, $R^2 = .91$. However, an analysis of covariance with ratio as the covariate and the percent of trials correct as the dependent variable indicated that the slope of the function for the human data was significantly different from that of the rhesus monkeys, $F(1, 59) = 49.85$, $p < .001$, and the capuchin monkeys, $F(1, 59) = 47.80$, $p < .001$. The two monkey species did not show a difference in the slope of their functions, $F(1, 59) = .47$, $p = .50$.

Discussion

Rhesus monkeys performed similarly to adult humans. For both species, there was no difficulty in judging which of the two sets contained the larger number of items. Capuchin monkeys performed at a lower level, although some individuals' performances approached the performance of the rhesus monkeys and the adult humans. The capuchins' initially lower performance may have been the result of differential rearing and testing histories, or the fact that they worked on the task for relatively shorter individual sessions than did the rhesus monkeys. Both monkey species also

demonstrated that the number of dots played a role in the judgments that were made as they performed equally well when number and amount were not confounded as they did when they were confounded. Thus, the monkeys were attending to the number of dots in each of the two sets and using that as the basis for their responses. This provides another demonstration that monkeys sometimes will use the number of items in stimulus sets as the primary stimulus dimension to which they respond (e.g., Beran, 2007a; Brannon & Terrace, 2000; Cantlon & Brannon, 2005, 2006).

Although all three species showed increased response times as a function of the ratio between sets, this was most pronounced for human performance. This outcome stands in contrast to previous research with humans in which there was not a relation between response time and numerical magnitude measured in terms of the ratio between the two sets (Thomas, Phillips, & Young, 1999). Perhaps humans in this study showed an effect of ratio on response time because of the stimulus movement in the two sets (Thomas et al. used static arrays). Additionally, the monkey data indicated that the increase in response times across the range of ratios was much shallower than in previous studies that reported such a relation (e.g., Cantlon & Brannon, 2005, 2006). Again, this may have been the result of presenting arrays of moving stimuli. Therefore, the relation between response time, trial difficulty, magnitude, and quantity comparison remains to be investigated further in both of these species because of these inconsistencies with previous studies. Such additional data also would be useful in better understanding the extent to which enumeration of these kinds of stimuli occurs in parallel as compared to being a serial process.

Experiment 4

In the final experiment, monkeys were required to track and enumerate only a subset of the dots in each set of moving stimuli. This meant that sometimes the set with the largest total number of items had the smaller target subset. This is a more difficult task as it requires a higher level of attention and resistance to distraction by nonrelevant stimuli. Such capabilities may be required in natural situations. For example, with static arrays, an animal might have to identify ripe fruits among unripe fruits. Here, the total number of food items should not play a role in the decision. With moving stimuli, a better analogy might be monitoring a specific type of prey species or predator among a larger group of animals when all are moving. Thus, the monkeys in this experiment had to segregate a subset of the stimuli and then enumerate only that subset while ignoring the other stimuli within each array.

Method

Participants and apparatus. The same rhesus monkeys and capuchin monkeys participated in this experiment as in Experiment 3. The apparatus was identical to all previous experiments.

Design and procedure. Sets of 1 to 12 dots were created and presented as in Experiment 1 and Experiment 3, with all items moving at randomly determined speeds and directions. Each dot was randomly assigned a size. In addition, each dot was randomly assigned as part of the target set (black dots) or the distracter set (red dots) with the only restriction that the target sets could not be equal in number between the two sides of the screen. Thus, each

set presented a differing number of red and black dots within it across trials. All other details of the trial presentation were identical to Experiment 3. Each monkey completed 1,000 trials.

Results and Discussion

Figure 6 presents performance for both species based on the difference (A) and ratio (B) between target sets (ratios were sorted into 1 of 9 bins ranging from .10 to .90). For each species, data are separated into two conditions. In the congruent condition, the array with the larger number of black (relevant) dots also had the larger total number of dots or the total number of dots in the two sets was equal. In the incongruent condition, the array with the larger number of black (relevant) dots had the smaller total number of dots. This condition is the critical condition in demonstrating that a species could track and enumerate a subset of the array because performance should not be lower compared to the congruent condition. The performance of the rhesus monkeys did not decrease for this special subset of trials compared to their overall performance, $t(8) = 1.11$ $p = .30$. However, the capuchins performed significantly lower in the incongruent condition, $t(8) = 4.99$, $p < .01$.

These data indicate that rhesus monkeys can segregate a subset of stimuli from an array of moving items and enumerate those stimuli only. These data support previous studies that have shown the ability of humans and nonhuman animals to attend to subsets of arrays in quantitative tasks (e.g., Halberda, Sires, & Feigenson, 2006; Pepperberg, 1987, 1994). Here, such subsets moved within larger arrays, and the monkeys were successful even when the total number of items in the two arrays was not a valid cue to the correct response. Capuchin monkeys had more difficulty with this condition, performing closer to chance levels. However, this did not mean that they were not attempting to segregate the relevant set of black dots. If they were only responding to the total number of dots in each set, performance in the incongruent condition would have been below chance levels as they would have been using an invalid cue.

General Discussion

Four major findings resulted from this study. First, two monkey species succeeded in selecting the larger of two sets of stimuli in which all stimuli were part of arrays of moving elements. Constant movement required tracking items within arrays while enumerating those items so as not to over- or underestimate array sizes. Rhesus monkeys and capuchins succeeded, although performance showed the typical outcome of decreasing performance as the ratio between sets increased (as predicted by Weber's law). Thus, estimation of each set's numerosity was approximate, not exact, suggesting that the enumeration process was not analogous to counting but was more similar to analogue magnitude estimation in which there was increasing variability in the estimation of set size as a function of true set size.

The second finding confirmed that this was a numerical task for the monkeys. When amount or area were eliminated as confounding cues with numerosity, performance remained as high as when those things were confounded. This is particularly compelling given that amount was readily available as a valid cue on the majority of trials completed by the monkeys. That they did not use those cues suggests that the monkeys were making judgments of
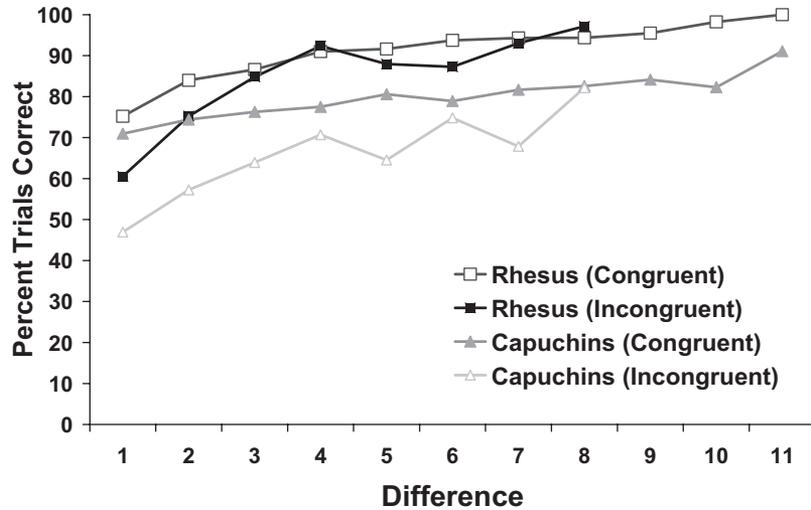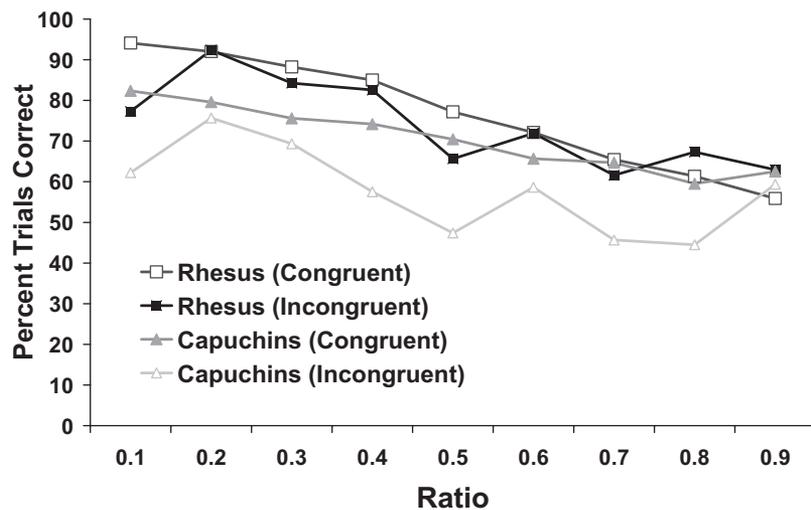
Figure 6. Mean performance at each difference (A) and each ratio (B) of the two target sets in Experiment 4 for the two monkey species. Data are shown for two conditions. The congruent condition involved trials in which the larger number of black dots was in the same array as the larger number of total dots or when the total number of dots was the same in both sets. The incongruent condition involved the larger number of black dots being in the array with the smaller total number of items.

the relative numbers of items in the sets. Thus, the task is one of relative numerousness judgments. This point also was confirmed in Experiment 2 where it was demonstrated that the complexity of the array movement was not used as a cue by rhesus monkeys when they successfully discriminated between one moving and one static set of dots and performance mirrored that of comparing two moving sets.

The third finding pertains to the ability of monkey species to enumerate subsets of stimuli within moving arrays. This was arguably the most complicated task that the monkeys were presented, as they had to focus attention on only a subset of the moving stimuli in each set while ignoring the distracting stimuli

and the effect of those stimuli on the overall number of items in that set. The high performance of the rhesus monkeys supports other data with children and nonhuman animals (Halberda et al., 2006; Pepperberg, 1994) that shows their capacity to separate different groups of stimuli within an array and then enumerate those subsets. The present data provide the basis for presenting future tasks in which monkeys must subdivide arrays or sum the total of two or more subsets of larger arrays. The current data do support the idea that numerosity of subsets is a salient property of heterogeneous arrays of stimuli.

The fourth finding pertains to differences between the two monkey species in their performance. Rhesus monkeys were much

more effective in enumerating subsets within two moving arrays than were capuchin monkeys. In fact, the direct comparison with human performance suggested little or no difference between humans and rhesus monkeys, even though humans were allowed to employ any strategies that they could, including counting routines and any subvocal enumeration processes. The difference between the monkey species may have been the result of differential rearing and experiential histories, as some of the rhesus monkeys in this experiment have served as subjects in other quantity judgment studies in which they completed thousands of trials. However, some of the rhesus monkeys (Luke, Obi, and Han) have only slightly longer testing histories than the capuchin monkeys, and they have roughly comparable experiences in terms of the computerized tasks they have been presented. In addition, it was also true that some capuchins performed at much higher levels than conspecifics, and they approached the performance level of the macaques. Therefore, it remains to be determined the extent to which rhesus monkeys and capuchins differ in their numerical competencies. Past research has indicated that capuchins are successful in numerical comparison tasks using methods devised and used with rhesus monkeys (e.g., Beran, 2008; Judge et al., 2005). Thus, additional comparative research with these species will be informative.

Overall, these experiments add a new level of numerical competence to that already established for nonhuman animals. Enumerating and comparing moving sets of stimuli, even when amount/area and the complexity of that movement are removed as cues, indicates a conflux of cognitive capacities that are needed to support such performance. There must be overlap between perceptual capacities of attending to and tracking stimuli, procedural capacities for enumerating those stimuli, and executive capacities for comparing those sets and making decisions. As such, this demonstrates a cognitive sophistication for quantifying stimuli that next can be expanded to additional modalities and situations so as to better understand how animals enumerate moving sets of stimuli.

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