A Comparison of Numerical Representation in Rhesus Macaques (*Macaca mulatta*) and Humans

Gin Morgan and Herbert S. Terrace, Ph. D.

Columbia University Department of Psychology and New York State Psychiatric Institute

INTRODUCTION

This experiment builds on previous numerical research with nonhuman primates. Our goal was to expand the range of numerosities on which rhesus macaques (*Macaca mulatta*) have been trained previously and to determine how a monkey represents those values. Results were compared to those of human subjects to compare enumeration mechanisms used on this task.

QUESTIONS

- Do monkeys use a serial or parallel enumeration mechanism?
- Do data conform to Weber's Law (and the analog magnitude mechanism it implies)?
- How similar are the mechanisms used by monkeys and humans on this task?

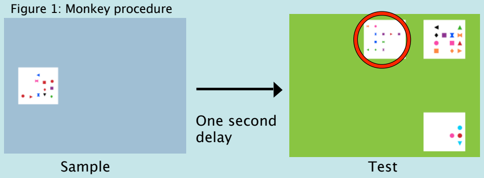
PROCEDURE

Monkey subjects

Five monkeys were originally trained on this task. Two monkeys, Augustus and Spike, completed all experimental conditions; their data is presented here. Monkeys were run daily in experimental chambers housed in isolated sound attenuated booths. Each booth contained a touch sensitive video monitor and an automatic pellet dispenser. Subjects were monitored via a closed-circuit video system. Each touch sensitive monitor was connected to an iMac G5 that presented all of the stimuli and recorded the accuracy and the RT data of each response. Correct responses were followed by a banana-flavored food pellet, a change in the color of the monitor, and a distinct sound. Incorrect responses were followed by a different distinct sound and a 4 second time out during which the screen was dark. The sample was shown in a random location on a blue background. Touching the sample extinguished it, and following a one second delay, the test screen displayed the target and distractors on a green background (Figure 1).

The numerical values of the sample and distractors were chosen randomly. Stimuli were composed of geometric figures that differed in size, shape, and color. Cues including shape, color, element configuration, cumulative surface area, and element density were progressively eliminated to ensure reliance on numerosity rather than secondary cues. Additionally, stimulus elements were heterogeneous in color and shape. Monkeys were tested with two stimulus continua: values 1-9 followed by values 1-15.

Figure 1: Monkey procedure



Human subjects

To compare performance between monkeys and humans for numerosities 1-15, Columbia undergraduates (n=17) completed the matching to sample task. Subjects worked in an isolated subject room and used a touch sensitive monitor. Subjects were not given explicit instructions to complete the task; instead, they began their session with 15 practice trials during which they were expected to discover the matching rule. Correct responses were followed by a pink screen and distinct sound; incorrect responses were followed by a different sound and a one second time out. Subjects were tested with numerosities 1-15, 2 distractors, a 0 second delay, heterogeneous stimulus color and shape, with random stimulus surface area, nonidentical sample and target configuration, and controlled element density. After completing a 15-trial block during which they had 6.0 seconds to respond to each screen, subjects completed 75 trials with only 3.5 seconds to respond to each screen in order to roughly equate the range of monkey and human RTs. After their computerized session, subjects completed a questionnaire regarding their enumeration strategies.

RESULTS

Accuracy (Monkeys)

Monkeys were tested with the stimulus range 1-9 followed by 1-15. Accuracy for both ranges is shown in Figure 2. When the stimulus ranges are plotted to equate continuum length, the accuracy functions are both qualitatively and quantitatively similar. Accuracy to end values at both ends of the continuum reflects a robust end effect. In addition to an end effect, accuracy is also mediated by the target-nearest distractor distance (Figure 3).

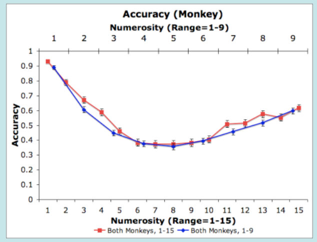


Figure 2: Accuracy for monkey subjects (n=2). Bars reflect standard errors.

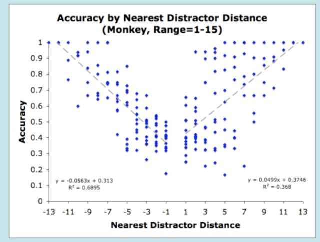


Figure 3: Accuracy by target-nearest distractor distance for monkey subjects (n=2)

RT (Monkeys)

Reaction times to the sample are shown in Figure 4. Reaction times to the sample do not increase with magnitude and instead show no effect of target numerosity. Median RTs for correct responses at test are shown in Figure 5. Reaction times at test are longer for intermediate values, again suggesting an end effect.

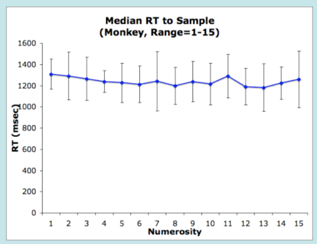


Figure 4: Median RT to sample for monkey subjects (n=2). Bars reflect standard errors.

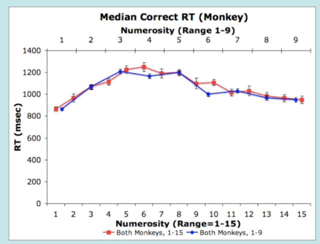


Figure 5: Median RT at test for monkey subjects (n=2). Bars reflect standard errors.

Accuracy (Humans)

Accuracy for human subjects (n=17) is shown for all trials with a 3.5 second time limit in Figure 6. High accuracy and questionnaire responses reflect the ability to subitize smaller values. Accuracy values for larger numerosities reflects an end effect.

RT (Humans)

Median reaction times for correct responses at test are shown in Figure 7. Like those of monkeys, RTs at test are longer for intermediate values, again suggesting an end effect.

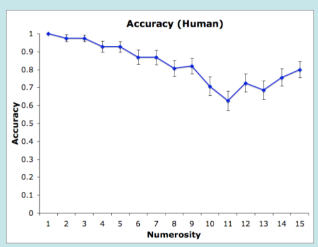


Figure 6: Accuracy for human subjects (n=17). Bars reflect standard errors.

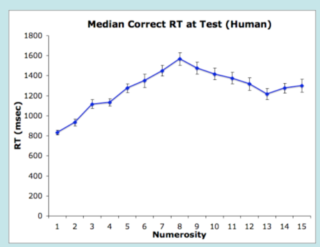


Figure 7: Median correct RT at test for human subjects (n=17). Bars reflect standard errors.

Response Variation (Monkeys and Humans)

Standard deviations for monkeys' responses do not increase systematically with stimulus magnitude (Figure 8). While the standard deviation values are different for ranges 1-9 and 1-15, the shapes of the functions are qualitatively similar. The coefficient of variation, calculated by dividing the mean response by the standard deviation for each numerosity, is shown for both monkeys and humans in Figure 9.

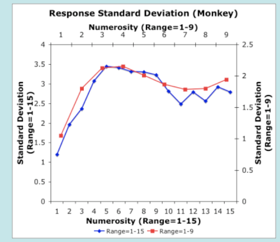


Figure 8: Standard deviation of responses for monkey subjects (n=2)

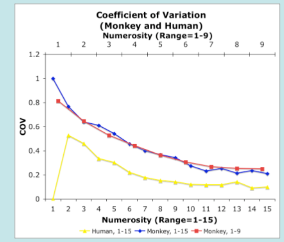


Figure 9: Coefficient of variation for monkey (n=2) and human (n=17) subjects

CONCLUSIONS

In monkeys, both accuracy and RTs reflect a robust end effect on both ends of the stimulus continuum. Due to the quantitative and qualitative similarity between response curves for both stimulus ranges (1-9 and 1-15), rhesus macaques appear to use a single estimation mechanism for all stimuli that is influenced heavily by relative continuum position.

When humans are given limited time to complete the task, reaction times reflect a similar influence of continuum position. In addition to subject self-report, accuracy for human subjects appears to reflect an ability to subitize smaller values but response patterns for larger values appear similar to those obtained from monkeys. Thus, while human subjects may use more than one enumeration mechanism to complete the task, estimation appears to be similar in both species.

If monkeys were to use an iterative enumeration mechanism, one would expect RTs to the sample to increase with increasing sample magnitude. Because RTs to the sample are not affected by magnitude, rhesus macaques appear to use a parallel enumeration mechanism.

Accuracy for monkeys shows a distance effect because average accuracy increases with increasing distance of the nearest distractor. Accuracy shows a similar ratio effect, with accuracy increasing with decreasing sample: distractor ratio (data not shown). It is possible, however, for results to show a distance or ratio effect without conforming to Weber's Law. This is true in the present studies because the standard deviation for responses does not increase with target magnitude and the coefficient of variation is not constant. Instead, the coefficient of variation is qualitatively similar for monkeys for both stimulus ranges and humans, again suggesting the importance of relative continuum position for estimation and similar estimation in both species.

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CONTACT

Gin Morgan, gmorgan@psych.columbia.edu