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Spontaneous number representation in semi-free-ranging rhesus monkeys

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Previous research has shown that animals possess considerable numerical abilities. However, this work was based on experiments involving extensive training, a small number of captive subjects and relatively artificial testing procedures. We present the results of experiments on over 200 semi-free-ranging rhesus monkeys using a task which involves no training and mimics a natural foraging problem. The subjects observed two experimenters place pieces of apple, one at a time, into each of two opaque containers. The experimenters then walked away so that the subjects could approach. The monkeys chose the container with the greater number of apple slices when the comparisons were one versus two, two versus three, three versus four and three versus five slices. They failed at four versus five, four versus six, four versus eight and three versus eight slices. Controls established that it was the representation of number which underlay their successful choices rather than the amount of time spent placing apple pieces into the box or the volume of apple placed in the box. The failures at values greater than three slices stand in striking contrast to other animal studies where training was involved and in which far superior numerical abilities were demonstrated. The range of success achieved by rhesus monkeys in this spontaneous-number task matches the range achieved by human infants and corresponds to the range encoded in the syntax of natural languages.

Keywords: number representation; primates; rhesus monkeys; language; infant

1. INTRODUCTION

Several non-human animal species have the capacity to represent number (Fernandes & Church 1982; Matsuzawa 1985; Boysen & Bernston 1989, 1995; Gallistel 1990; Pepperberg 1994; Brannon & Terrace 1998). Previous studies which have revealed numerical knowledge in animals have generally involved extensive training, often involving several hours, months or even years. This fact has led some (Davis & Memmott 1982; Davis & Perusse 1988) to speculate that number is not a salient aspect of the environment for animals and that the representational capacities reflected in these studies are constructed during the process of training. Others (Gallistel 1990; Gallistel & Gelman 1992; Boysen 1997; Dehaene 1997) have noted the importance of number representations in the service of computing rates and probabilities and suggested that number is automatically, spontaneously represented as animals interact with their worlds. This speculation has never been tested.

Here we report on, to the authors' knowledge, the first systematic studies of spontaneous (untrained) number representation in a non-captive animal, the rhesus monkey. Although some studies have tested animals without training, they have not explored the problem of number in a systematic way. However, they do show that animals make spontaneous quantity comparisons (more or less food or competitors) (Menzel & Halperin 1975; McComb *et al.* 1994; Hauser *et al.* 1996; Silberberg & Fujita 1996) and, thus, were important in shaping our experimental approach.

Our study had two goals. First, we sought to establish at least one context in which the number of objects presented in a given event might be spontaneously encoded. We selected a foraging problem involving two choices, given that laboratory results with chimpanzees and rhesus monkeys have shown preferences for nine versus eight items after some training on smaller quantities (Washburn & Rumbaugh 1991; Rumbaugh & Washburn 1993; Boysen & Bernston 1995). Second, we sought to establish the limits of this capacity, both as a point of comparison with training experiments on animals and their number representations, as well as with human infant studies involving spontaneous number representation prior to the acquisition of language.

2. METHODS

The subjects were adult male and female rhesus monkeys (*Macaca mulatta*) living on the island of Cayo Santiago, Puerto Rico (Rawlins & Kessler 1987; Hauser & Carey 1998). All animals were readily identified by natural markings, as well as tattoos and ear notches.

Two researchers placed themselves 2 m apart and 5–10 m away from the test subject. Each researcher then showed the monkey a distinctively coloured, opaque box and emphasized that it was empty by tipping it sideways and placing an open hand inside; each researcher then placed the box on the ground in front of his/her feet. One researcher then placed one or more objects into the box, making sure that the monkey watched the events. When the objects were in place, the researcher stood up and looked down. Subsequently, the other researcher placed one or more objects into his/her box and then stood up and looked down. Having completed these events, both researchers then turned and walked away in opposite directions, walking at an

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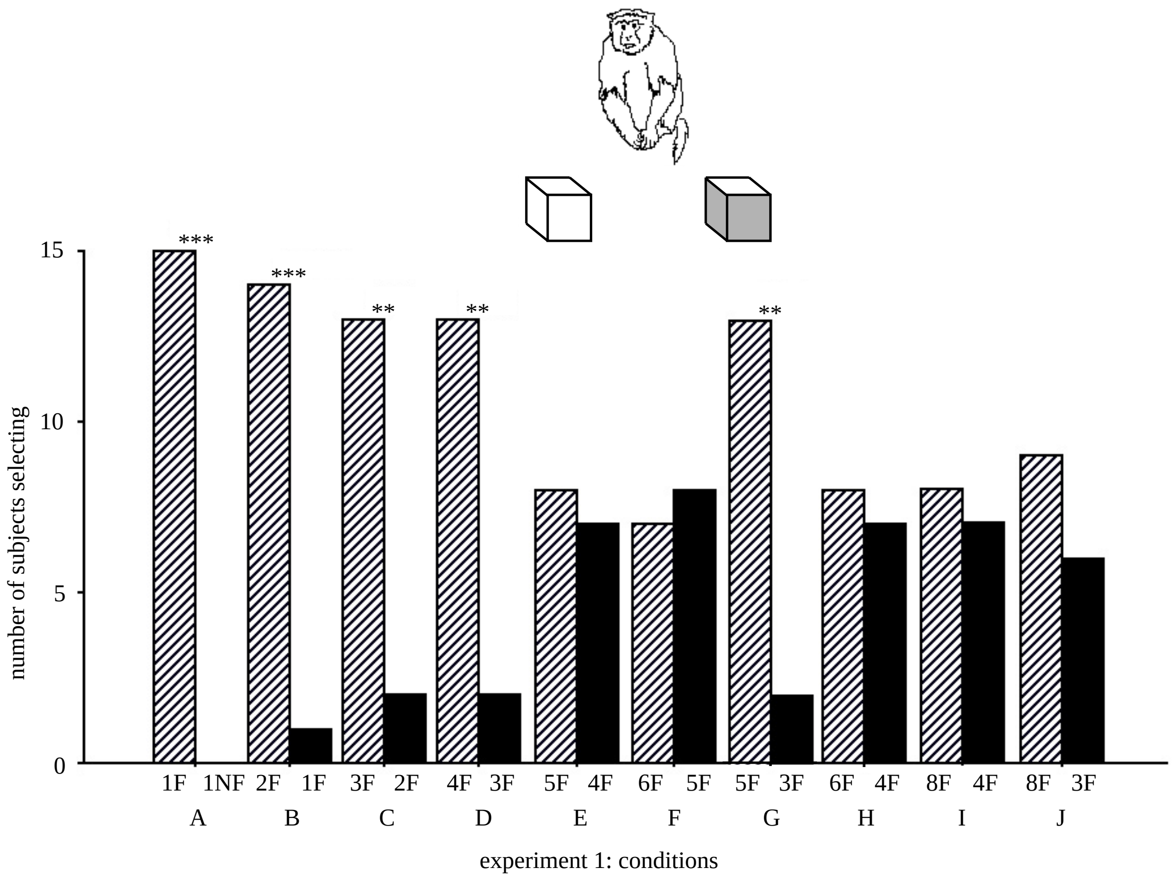

Figure 1. The results from experiment 1. Fifteen subjects were run in each condition in experiment 1 and the y-axis plots the number of subjects picking the larger (striped bars) over the smaller number (black bars) of apple slices. Statistical significance was tested with a one-tailed sign test, with significance set at the $p<0.05$ level. Condition A involved the presentation of one slice of apple (one-eighth of an apple; F = food) versus one rock (NF = non-food). All other conditions in experiment 1 involved the presentation of different food quantities, some sets differing by only one apple slice (conditions A–F), while others differed by as much as two or more times the quantity in the other box (conditions G–J). All quantities were presented sequentially. $^{***}p<0.001$, $^{**}p<0.004$.

even pace; by walking away, the subjects were provided with an opportunity to approach one of the boxes.

Each experimental condition was designed to assess whether rhesus monkeys would spontaneously quantify the number of objects and contrast the relevant quantities once they are out of sight. In condition A of experiment 1, a target subject watched as one researcher placed a rock into his box, followed by the other researcher placing a slice of apple (one-eighth of an apple) into her box. Given the success in this test, the rest of the conditions in experiment 1 explored larger numbers of apple slices, with choices differing from just one apple slice (conditions B–F) to choices differing in more than one apple slice (conditions G–J); the food stimuli were always slices of apple (one-eighth of an apple each).

To ensure that the representations in the present studies were spontaneous, we attempted to test each animal only a single time (see § 3). To ensure that the representations were numerical, the animals saw each apple slice for only a few seconds put one by one into each box from a distance of 5–10 m. Although we assumed that the monkeys would attempt to maximize the amount of apple obtained, we also assumed that the way they would do so was by making an 'equal volume' assumption, estimating the total amount from the number of pieces; this assumption was directly tested in experiment 2.

Within each condition, we counterbalanced the order of presentation of object quantities, the side in which different quantities were presented and the researcher responsible for presenting the larger or smaller quantity. Animals who did not watch every placement were not allowed to make a choice. In addition, animals who were chased away by others or who failed to make a choice for any other reason were replaced. Fifteen individuals were tested in each condition and a one-tailed sign test was used to assess whether the subjects preferentially selected one quantity over another.

3. RESULTS

Fifty-four of the 225 trials included monkeys who had been run in the procedure on at least one other occasion, sometimes over a year earlier. The performances of those monkeys run more than once did not differ significantly from those run only once. The average success in conditions of group success by monkeys who had been tested before was 81%, compared with 89% by monkeys for which the trial was their first. The average success in conditions of overall group failure by monkeys who had been tested before was 49%, compared with 54% by monkeys for which the trial was their first. For experiment 1, 189 subjects were tested to obtain a sample of 135.

In condition A, 15 out of 15 subjects approached the box with the apple (figure 1). The monkeys had no problem discriminating the objects and were not influenced by the order of presentation, nor by the researcher presenting each object. In condition B, the subjects preferentially approached the box with two slices over the box with one slice. This pattern of preferentially picking the larger quantity continued up to condition D, which involved four versus three slices. The monkeys also succeeded in condition G, which involved five versus three slices. However, in all subsequent conditions, in which one or both numbers exceeded four slices, there were no statistically significant preferences. Thus, even with a twofold ratio between the two quantities (eight versus four and eight versus three slices), the monkeys chose at random.

As each subject was tested only once, the subject could not have learned that it would be offered choices between different apple quantities and that it would be allowed to obtain one of the two quantities. Rather, it must have spontaneously kept track of the placement of apples into the box and represented the numbers of slices in memory, when those numbers were one, two or three slices. Further, the monkeys must have been able to compare their representations of the two numbers to establish their ordinal relations, for they chose the box with the larger number of apple slices. This suggests that rhesus monkeys have access to a spontaneous system of representation, which encodes the numerical differences between sets of one, two and three objects and contrasts three objects from either four or five objects as well.

The tests in experiment 1 were confounded by time. In each of the successes, with the exception of condition A, the larger quantity was perfectly correlated with the length of the presentation time; for example, it takes longer to place three slices into the box than two slices. It is unlikely that the monkeys were merely encoding time, for the temporal difference between the failures at three versus eight and four versus eight slices were greater than those between three versus four or three versus five slices. To eliminate the possibility that the relative length of the events was determining choice conclusively, we ran experiment 2, which involved four conditions in which the number of objects placed into each box was the same, but one box always contained one more piece of apple; the general procedure was the same as in experiment 1. Thus, for example, condition K involved placing two slices of apple into one box and one slice of apple plus one rock into the other box. The other choices were three apple slices versus two apple slices plus a rock (condition L), four apple slices versus three apple slices plus a rock (condition M), and five apple slices versus four apple slices plus a rock (condition N). Since the monkeys failed in condition E of experiment 1 (five versus four slices), they were expected to fail in condition N of experiment 2. This would ensure that successes in conditions J–L, if obtained, were not simply due to the monkey avoiding the box with the rock. As a further test of this possibility, condition O was run in which we contrasted three apple slices plus a rock versus two apple slices. A final condition, condition P, was run to assess whether the monkeys were choosing on the basis of number or volume. The subjects were thus given a choice between one-half of an entire apple or three pieces, each one-sixth of an apple. If they directly track total volume, they should choose randomly. If they encode number and assume equal volume, they should choose the box with three slices.

One-hundred and forty-four adult rhesus monkeys were tested to obtain a sample of 90 subjects in experiment 2. The subjects preferentially selected the box with the greater quantity of food in just those cases in which the contrast between sets of apple slices were the same as those in which the monkeys succeeded in experiment 1 (conditions K–M, plus condition O, corresponding to conditions B–D in experiment 1) (figure 2). The monkeys succeeded even though the actual number of objects placed in each box was the same (conditions K−M), the total time spent placing objects into each box was the same, the total amount of activity associated with each box was the same and so on. The monkeys attended to the apple slices, comparing the boxes on the basis of the relative number of apple slices while ignoring the rock. The addition of the rock did not disrupt performance whatsoever; the success rate was 89% for both conditions B–D in experiment 1 and for conditions K–M in experiment 2. Choice for the greater number of apple pieces broke down at five slices versus four slices plus a rock (condition N), paralleling the results from condition E in experiment 1. This last result, along with the success in condition O shows that success in experiment 2 was not simply due to choosing the box without a rock. Finally, in condition P the monkeys chose the box with three slices over the equal volume choice of half an apple. Under these test conditions, they are not able to encode the total volume of apple directly and, thus, chose on the basis of the number of pieces of apple.

4. DISCUSSION

This study adds two new findings to the rich literature on animal representation of number (Gallistel 1990; Boysen 1997; Dehaene 1997; Hauser & Carey 1998): number is represented spontaneously and spontaneous representations, at least under the present experimental conditions, seem to be limited to comparisons among one, two, three and more objects. First, consider the evidence that the distinctions between one, two and three objects are spontaneously represented by rhesus macaques. These were unique events for the subjects in our study and there were no cues that they were being tested on a number experiment. In the course of each trial, a subject formed an accurate representation of small numbers of apple slices and used this representation to select the box with more slices.

Second, our subjects' performance broke down at comparisons which involved numbers greater than four objects. This pattern of results suggests that the spontaneous representation of number deployed by rhesus monkeys in this situation is not a scalar, analogue-magnitude system of representation (Meck & Church 1983; Dehaene & Changeux 1993). In such representational systems, success at four versus six objects should be comparable with the level of success at two versus three objects and clearly less than four versus eight or three versus eight objects. However, the monkeys were completely at chance at four versus six or eight and at three versus eight objects in the face of robust and repeated

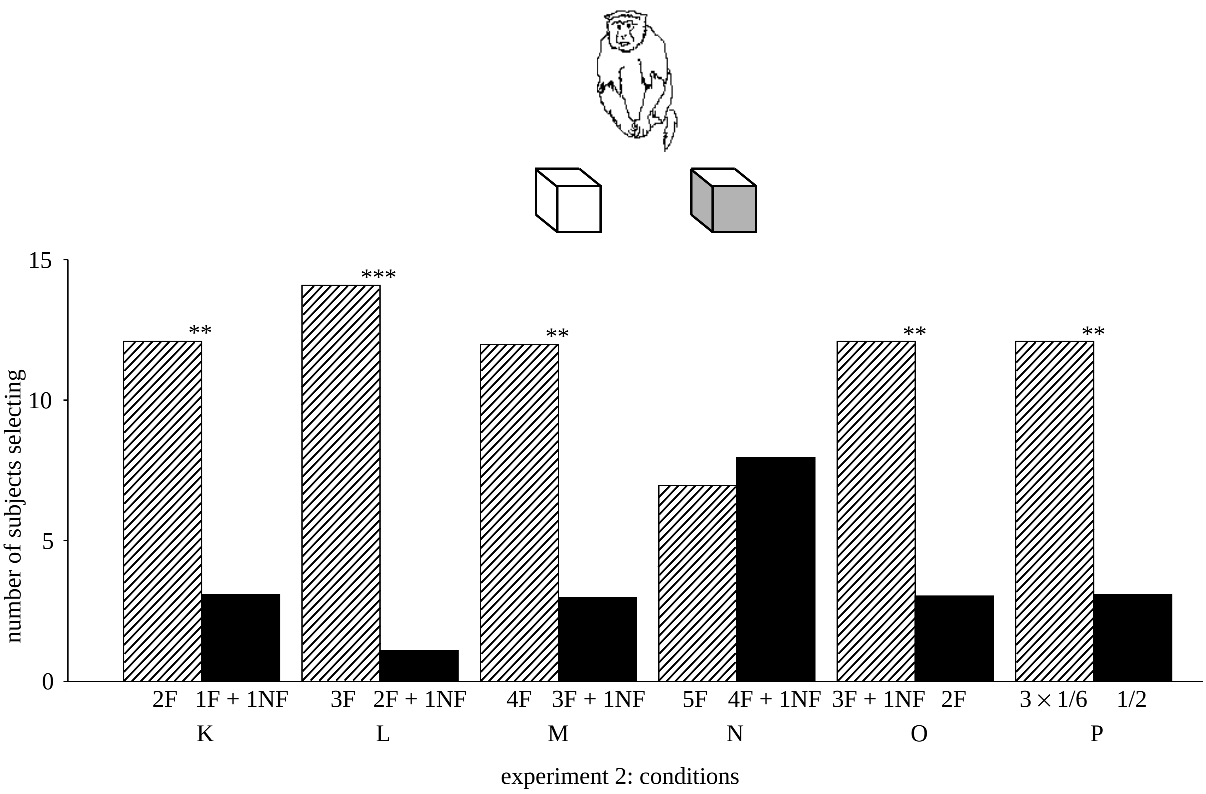

Figure 2. The results from experiment 2. Fifteen subjects were run in each condition and the y-axis plots the number of subjects picking the larger (striped bars) over the smaller number (black bars) of apple slices. F = food (apple slices) and NF = non-food (rock). All quantities were presented sequentially. $^{***}p < 0.001$, $^{**}p < 0.004$.

success at two versus three objects. Thus, although animals, including rhesus macaques, have the capacity to form analogue-magnitude representations of number which well-exceed three (Matsuzawa 1985; Washburn & Rumbaugh 1991; Pepperberg 1994; Brannon & Terrace 1998), it seems that this representational capacity is not spontaneously deployed under the circumstances of the present studies.

Rather, the patterns of successes and failures are what would be expected if the spontaneous system of representation deployed under these circumstances consists of symbols for each slice in each box, the memory representations then being compared on the basis of one-to-one correspondence (Simon 1997, 1999; Uller *et al.* 1999). In this hypothesis, the limit of three or four objects is a limit of parallel individuation with a model of a given set of objects (Trick & Pylyshyn 1994). Such a system represents number in a weaker sense than analogue-magnitude representational systems, in that it contains no explicit symbols for number. However, it does represent number as it requires criteria of individuation and numerical identity and supports number-relevant computations such as those which determine more/less in the present experiments. What is most intriguing about the rhesus monkey's limited capacity for spontaneous number representation is that it parallels the capacities of human infants tested under comparable experimental conditions (Hauser & Carey 1998; Wynn 1998; Uller *et al.* 1999).

The numerical distinctions spontaneously represented correspond to those encoded in the syntax of natural languages. Specifically, languages that encode number grammatically distinguish singular/plural, singular/dual/plural and (rarely) singular/dual/trial plural (Hurford 1987; Dehaene 1997; Butterworth 1999). The syntax of number concerns the quantification of small sets of individuals, does not require an explicit, integer-list, representational system and is likely to be built, both evolutionarily and ontogenetically, upon parallel indexing of small sets of numerically distinct individuals.

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