

Numerical representations in primates

(concepts/arithmetical abilities/comparative methods)

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ABSTRACT Research has demonstrated that human infants and nonhuman primates have a rudimentary numerical system that enables them to count objects or events. More recently, however, studies using a preferential looking paradigm have suggested that preverbal human infants are capable of simple arithmetical operations, such as adding and subtracting a small number of visually presented objects. These findings implicate a relatively sophisticated representational system in the absence of language. To explore the evolutionary origins of this capacity, we present data from an experiment with wild rhesus monkeys (*Macaca mulatta*) that methodologically mirrors those conducted on human infants. Results suggest that rhesus monkeys detect additive and subtractive changes in the number of objects present in their visual field. Given the methodological and empirical similarities, it appears that nonhuman primates such as rhesus monkeys may also have access to arithmetical representations, although alternative explanations must be considered for both primate species.

Over the course of evolution, the human brain and mind have been subjected to selection pressures that have resulted in a suite of species-typical design features. Of these, language is often characterized as not only typical of the human species but unique. Although nonhumans may share some of the design features of human language (e.g., hemispheric asymmetries; refs. 1–3), they appear to lack those features (e.g., a universal grammar) that are foundationally important for the expressive power of our communication system (4, 5). An important question, however, is what kinds of conceptual representations are either necessary or sufficient for language acquisition. This question is relevant to those interested in the evolution of the human species as well as those interested in the developing human infant. Along these lines, the concept of number is one representational domain that has received considerable interest within the past 10 years by developmentalists concerned with the processes guiding the child's changing cognitive abilities (6–9) and by comparative biologists and psychologists interested in nonhuman animal cognition (10, 11). Although nonhuman animals clearly have a rudimentary numerical system, an ability one would expect at some level given the adaptive significance of keeping track of the number of animals in one's group or the number of feeding sites visited on a foraging route, it is difficult at present to compare these results with those obtained on human infants due to potentially critical differences in methodological approaches. Thus, whereas studies of numerical competence in human infants have employed a preferential looking procedure that taps into spontaneous cognitive processing, studies of nonhuman animals have used extensive training procedures, thereby imposing greater constraints on the nature of the putative representation or category. To compare cognitive abilities across

species, we require comparable methods, and the preferential looking paradigm is ideally suited.

The preferential looking paradigm has been used extensively by developmental psychologists to gain insights into how infants represent both the spatial and temporal properties of objects, how they come to understand the nature of causal relationships, and the extent to which they can perform numerical operations on auditory and visual stimuli in their environment (12–15). The logic underlying this paradigm is that individuals will look longer at events that are impossible or unexpected—that in some sense violate their knowledge of the world. Thus, when a magician saws through a live human body, separates the two halves, and then reconstitutes them without damage, adults are surprised because our expectations about human bodies have been violated. If infants share such knowledge, then their expectations would also be violated by the magician's act and thus would show surprise by an increase in looking time compared with events that are consistent with their knowledge.

This paper focuses on the capacity to perform simple arithmetical operations—one form of numerical competence. A pioneering study by Wynn (9) indicated that human babies understand that one object plus one object is exactly two objects and similarly that two objects minus one object is precisely one object. Thus, for example, infants first saw an object placed on an empty stage, then saw a screen lowered to conceal the object, followed by the placement of a second object behind the screen. When the screen was removed, they looked longer when only one or three objects were present than when two objects were present. Our experiments were designed to mirror Wynn's addition and subtraction tests and therefore to directly assess her claim that simple arithmetical abilities are innately determined in humans.

Experiments were conducted on a population of wild rhesus monkeys living on the island of Cayo Santiago, Puerto Rico (16, 17). Trials were obtained opportunistically whenever subjects (adult males and females) remained in one position for a sufficiently long time to present our stimuli (purple eggplants). At the start of our experiments, we did not expect each subject to remain in one place long enough to test on repeated trials. Thus, and in contrast to studies with human infants where individuals receive a set of familiarization or habituation trials followed by a set of test trials, each rhesus subject was tested only on a single trial of the *addition* ($1 + 1$) conditions (9). Under this procedure (Fig. 1), we predicted that individuals would look longer during presentations that violated the laws of addition (T3) than during possible conditions that were either consistent with the laws of addition (T1–T2) or involved object presentations in the absence of arithmetical manipulations of those objects (F1–F4). In conditions F1 and F2, subjects watched either one or two eggplants placed in the display box with no screen. In conditions F3 and F4, subjects first saw the box with the screen down and then, as the screen was removed, saw either one or two eggplants; subjects should not be surprised here because they have no prior expectations about what is behind the screen. Conditions T1–T3 all start with an empty display box, followed by the lowering of a screen.

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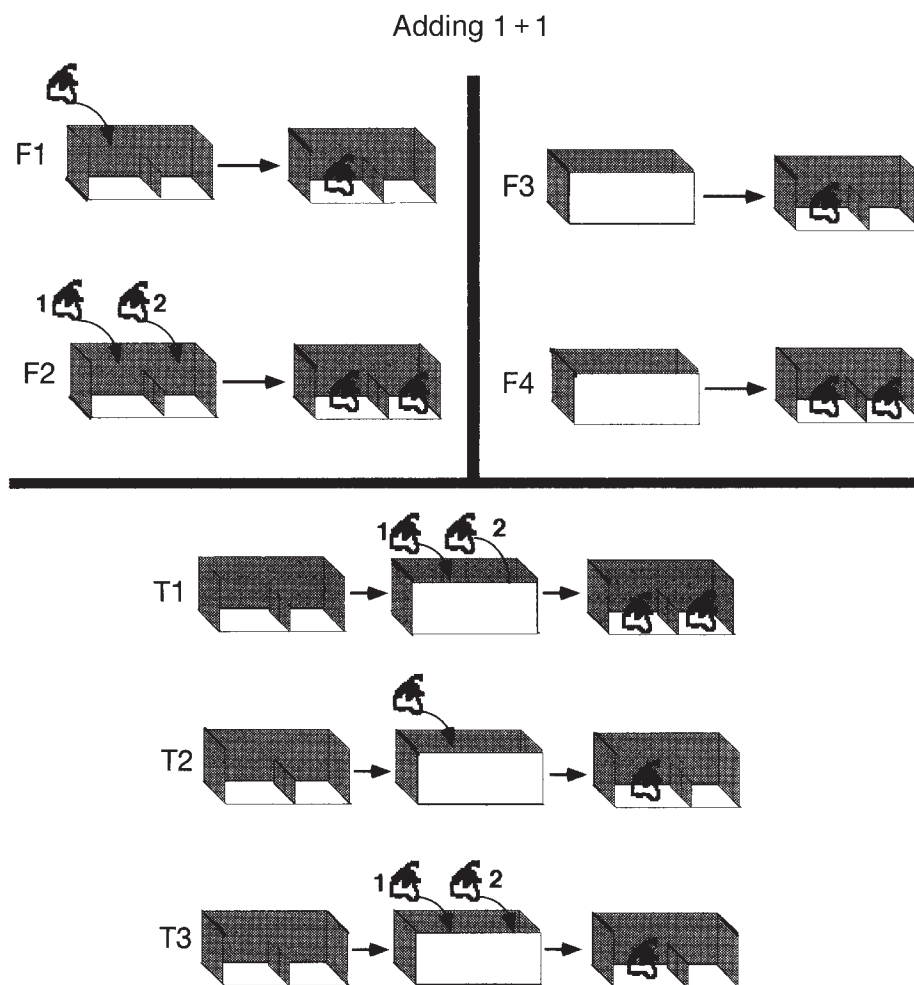


FIG. 1. Experimental design for tests of addition in rhesus monkeys. The display structure, with two compartments separated by a low partition, was made of white foam core with a moveable screen. The rest was secured to a wooden base. On the back side of the screen was a hidden pocket. This made it possible to insert an object into the display, only to remove it when the screen was raised. In the "possible" condition, all objects inserted were then in view when the screen was raised. In the "impossible" condition, there was a discrepancy between what subjects saw inserted, and what was revealed when the screen was removed. For the second set of experiments on addition, F1–F4 are familiarization (F) conditions. T1–T3 are the experimental tests (T); T3 is the only impossible condition. For all of the test conditions, the eggplant(s) remained behind the screen, and thus out of view, for 5–15 s. Three observers were involved in each experiment. One individual set up and presented each condition, while a second individual filmed the test subject's face. The third observer was responsible for detecting potentially distracting events (e.g., another individual approaching, a fight breaking out) that might significantly affect the monkey's looking response; trials were aborted if the subject was distracted by an external event.

In T1, subjects saw one eggplant lowered behind the screen and then, when the screen was removed, saw one eggplant inside the box. In T2, subjects saw first one eggplant and then a second lowered behind the screen; when the screen was removed, they saw two eggplants. T3 is considered the only impossible condition because of the discrepancy between the number of eggplants that were placed into the box (i.e., two) and the number of eggplants displayed once the screen was removed (i.e., one); this discrepancy is achieved by placing one of the eggplants in a concealed pouch behind the screen. Forty-eight adults (31 males and 17 females) viewed a single possible condition trial and 13 adults (9 males and 4 females) viewed a single impossible condition trial.

For all conditions, records of looking time were derived from a 10-s period. In F1 and F2, this period was initiated as soon as the display was placed in view; in F3 and F4, as well as T1–T3, the recording period started as soon as the screen went up, revealing either one or two eggplants.

Results indicated that subjects looked significantly longer during the presentation of the impossible condition (mean = 168.7 frames) than during the presentation of possible conditions (mean = 79.9 frames; $t = 4.91$; $P < 0.0001$). Moreover, a

significant effect was preserved when each of the two possible T conditions were compared with the impossible T3 condition (T1 vs. T3, $t = 4.83$; $P < 0.0001$; T2 vs. T3, $t = 3.41$; $P < 0.003$). This comparison is important because conditions T1 and T3 share the same setup steps (i.e., empty display, screen down, two objects displayed consecutively), whereas T2 and T3 share the same end product display (i.e., one object in view in the display area). Thus, T3 differs from T1 and T2 in that there is a discrepancy in the number of objects placed behind the screen and the number of objects remaining in the display box when the screen is removed.

Having completed the single trial tests, it was clear that some subjects would remain in one place for a sufficiently long time to permit multiple presentations. We thus changed the design of our experiment to more closely approximate those conducted on human infants and especially those that start with a series of familiarization trials and then end with a series of test trials (9, 12, 14). Specifically, for our test of $1 + 1$, each individual from a new set of subjects ($n = 20$ adult males and 19 adult females) was familiarized (F) with two different conditions (F1–F4) and was then presented with one of the three test (T) trials (T1–T3); thus, a complete session consisted of three trials. The familiarization trials were important for they con-

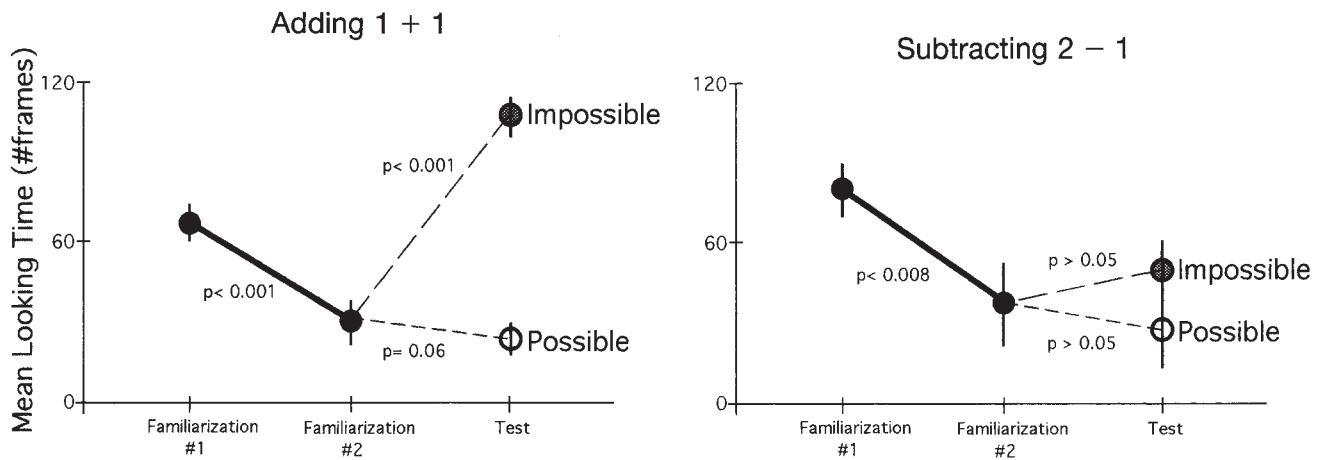


FIG. 2. Changes in mean looking time (number of frames/s) over two familiarization tests (solid circles) and then either one possible (open circle) or one impossible (shaded circle) test; standard errors are shown. (Left) The 1 + 1 addition experiment. (Right) The 2 – 1 subtraction experiments. Looking time was scored blind with regard to condition. This was achieved by first acquiring video recordings onto a Macintosh Quadra 950 using a Radius VideoVision digitizing board and Adobe Premiere 4.0 software. Once a trial was acquired, the onset and termination of the 10-s period was flagged with a marker. After all trials were acquired, an observer scored the number of frames (30 frames per s) in which the subject looked (i.e., direction of eye gaze) toward the display. Looking time data were matched with the test conditions, and statistical analyses were conducted. We examined the relationship between test condition and the total looking time for the 10-s period.

trolled for the possibility that individuals might find two eggplants more interesting than one eggplant. Subject sample size per test condition was T1 = 15, T2 = 12, T3 = 12; the time between successive trials within a session ranged from 10 to 30 s.

Results (Fig. 2) from the familiarization trials indicated that there was a significant decrease in looking time from familiarization trial one to two ($t = 4.29; P < 0.0001$). When a possible test condition (T1, T2) followed, there was a nonsignificant

decrease in looking time. In contrast, when the impossible condition followed, there was a significant increase in looking time ($t = 6.95; P < 0.0001$).

The final experiment tested rhesus monkeys in a 2 – 1 subtraction design (Fig. 3). A total of 19 new individuals (12 males and 7 females) were tested. Each subject received two familiarization trials, either F3 or F4 and then either F1 or F2. Subsequently, they were presented with either the possible (T1) or impossible (T2) test condition. Subjects showed a sig-

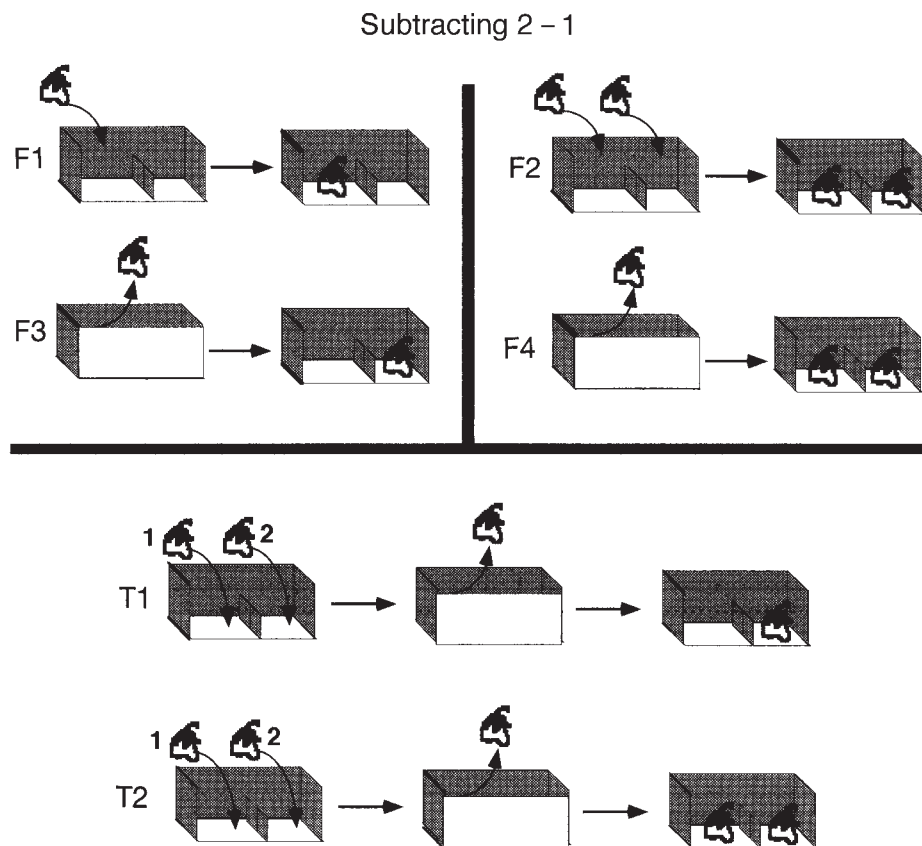


FIG. 3. Experimental design for 2 – 1 subtraction test. F1–F4 represent familiarization conditions. T1 is the possible test condition and T2 is the impossible test condition. See Fig. 1 legend for further description of events.

nificant decrease in looking time from the first to the second familiarization trial ($t = 3.58$; $P < 0.008$; Fig. 2). In contrast to the addition tests, there was significantly more variability in looking time scores on the subtraction test trials. Thus, the parametric t test failed to reveal a significant change in looking time from the second familiarization trial to either T1 ($n = 11$) or T2 ($n = 8$). However, a nonparametric sign test revealed no change in looking time from the second familiarization to T1 but a significant increase in looking time to T2 ($P < 0.02$). Thus, although the magnitude of change was not significantly different, 7 of 8 individuals showed an increase in looking time from the familiarization to the impossible condition; only one individual showed an increase in looking time for the possible condition.

Results indicate that in one population of wild rhesus monkeys, adults appear to respond differently to the presentation of events that violate simple arithmetical laws and those that are consistent with such laws. Specifically, following the initial decrease in looking time during familiarization trials, subjects showed an increase in looking time to impossible, but not possible, events for both $1 + 1$ and $2 - 1$. Methodologically, our experiments are similar to those presented by Wynn (9) in that a preferential looking procedure was used to assess knowledge of arithmetic, and the experiments were restricted to the addition or subtraction of a small number of objects. They differ, however, in one potentially important way: whereas the infants were tested in an object first design for the addition experiments, the rhesus monkeys were tested in a screen first design. In other words, whereas the infants always saw an object first followed by a screen and then a second object, rhesus monkeys saw an empty stage and were then required to maintain a representation of two objects being placed sequentially behind the screen. With the screen first design, human infants do not succeed until the age of ≈ 10 months (C. Uller and S. Carey, personal communication).

At this juncture, two interpretations of the data are possible. If the findings on human infants are taken as evidence of a limited, innately specified arithmetical ability (9), then the present data on rhesus monkeys reveal that other primates may have comparable abilities. Additional support for this line of thinking comes from studies of counting in other nonhuman primates and nonprimate vertebrates (10, 11) and preliminary evidence that cotton-top tamarins, a small New World monkey, are also capable of passing the arithmetic tests with a preferential looking paradigm (C. Uller, M.D.H., and S. Carey, unpublished data). An alternative interpretation, however, is that the paradigm used here and in the infant studies does not necessarily reveal arithmetical abilities in either species. Instead, it is possible that high-level perceptual representations retain information about previously seen objects even when they become temporarily occluded and that such representations may be rich enough to encode and distinguish between several such occluded objects at once. This capacity would be highly adaptive to both species but would not require an arithmetical concept.

Future studies must focus on distinguishing more precisely between arithmetical and perceptual representations in both human and nonhuman primates. For example, one condition run on infants (9), and yet to be run on rhesus monkeys,

involves a $1 + 1 = 3$ display. Infants look longer at this display than at $1 + 1 = 2$, indicating that they are not simply showing surprise at "more" objects. They seem to expect that $1 + 1$ is precisely 2 and nothing more—at least for solid objects. In addition to this manipulation, it will be important to show that, in both species, individuals are actually representing individual objects (18) rather than an overall change in the visual display. Thus, in the addition experiments, one could hide two eggplants behind the occluder and, when it is lifted, reveal a single large eggplant, equal in surface area to the two smaller ones. If subjects maintain a low level of looking, comparable to the familiarization trial, then this suggests that they were tracking a simpler perceptual feature (e.g., amount of purple) rather than the individual objects. Such experiments remain to be done in infants (18), rhesus monkeys, and cotton-top tamarins.

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