

Evolutionary and developmental foundations of human knowledge: a case study of mathematics

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1. The core knowledge thesis

What are the brain and cognitive systems that allow humans to play baseball, compute square roots, cook soufflés, or navigate the Tokyo subways? It may seem that studies of human infants and of non-human animals will tell us little about these abilities, because only educated, enculturated human adults engage in organized games, formal mathematics, gourmet cooking, or map-reading. In this chapter, we argue against this seemingly sensible conclusion. Instead, we suggest that when human adults exhibit complex, uniquely human, culture-specific skills, they draw on a set of psychological and neural mechanisms with two distinctive properties: they evolved before humanity and thus are shared with other animals, and they emerge early in human development and thus are common to infants, children, and adults. These core knowledge systems form the building blocks for uniquely human skills. To understand what is special about human intelligence, therefore, we must study both the core knowledge systems on which it rests and the mechanisms by which these systems are orchestrated to permit new kinds of concepts and cognitive processes.

What is core knowledge? A wealth of research on non-human primates and on human infants suggests that a system of core knowledge is characterized by four properties (Hauser, 2000; Spelke, 2000). First, it is domain-specific: each system functions to represent particular kinds of entities such as conspecific agents, manipulable objects, places in the environmental layout, and numerosities. Second, it is task-specific: each system uses its representations to address specific questions about the world, such as “who is this?” [face recognition], “what does this do?” [categorization of artifacts], “where am I?” [spatial orientation], and “how many are here?” [enumeration]. Third, it is relatively encapsulated: each core knowledge system uses only a subset of the information delivered by an animal’s input systems and sends information only to a subset of the animal’s output systems. Finally, its operation is relatively automatic and impervious to explicitly held beliefs and goals¹. Each of these properties gives rise to a set of *signature limits* that cognitive and brain scientists can use to identify particular core systems and their products across development and evolution.

In this chapter, we use the domain of number to illustrate how core knowledge systems are assembled to permit uniquely human cognitive advances in mathematics. We first review the comparative literature on animals and developmental studies of infants. This research provides

¹ We assume here that even animals that lack belief-desire psychology [theory of mind] nonetheless have numerous actions that are volitional, planned and goal directed and that the psychological mechanisms mediating these sorts of actions do not impinge upon the output systems guiding the relationship between core knowledge and action.

evidence for two core knowledge systems that serve as building blocks for the number concepts of educated humans: a system for representing exact small numbers of objects or events and a system for representing large approximate numerical magnitudes. We next show that as human children develop, they use these systems to construct the first uniquely human number concepts: the natural numbers. Finally, we explore how the core knowledge systems function in educated human adults, permitting us to embrace concepts and engage in cognitive processing that is unique in the living world.

2. Knowledge of number

Natural number concepts are so simple and clear to human intuition that one might suppose that they are shared by many animals and rooted in early human development. Both suppositions, however, are wrong. *Homo sapiens sapiens* is the only extant species that ever fully comprehends natural number concepts, and this understanding emerges only at about four years of age. Even the most highly trained chimpanzees and the most nurtured and educated two year old children fail to do so. What makes the natural number concepts so difficult for animals and young children to understand?

One way to see how difficult the natural number concepts are is to consider how children learn to express them through verbal counting. Although children in many cultures begin to engage in verbal counting as young as two years of age, most children do not understand either the meanings of number words or the workings of the counting routine until two years later. Children construct this understanding laboriously, well after they master the script of the counting routine. For example, a 2.5-year-old child who can count six toy fish reliably typically knows only the meaning of the first word in her counting routine: asked for "one fish," she will pick one and show it; asked for any other number, she will grab and show a handful of a number greater than one fish but otherwise unrelated to the correct cardinal value (Wynn, 1990). Furthermore, if a child at this age is told that the pile contains "four fish" and then watches as two fish are removed, she will maintain that the pile still contains "four fish" (Condry, Gramzow, & Cayton, 2003). Although she uses the counting words correctly in the count routine, she evidently interprets each word above one as simply meaning "more than one." With months of counting experience, as well as other cognitive advances that are running in parallel, children progress from understanding the meaning of "one" to understanding "two," and then "three"; this progression is highly systematic with no evidence of children learning other numbers in the integer count list first, nor learning the meaning of three before they learn the meaning of two (Wynn, 1990). After this slow, systematic, stepwise progression, children take a leap forward. They form the induction that each word in the counting routine gives the cardinal value of a set composed of a specific number of individuals, that each word denotes a set with one more individual than the previous word, and that the succession of cardinal values picked out by the number words can be continued indefinitely, with no upper bound. By age 5, preschool children can apply this knowledge robustly, even to number words outside their counting range (Lipton, 2003).

A second way to see how difficult the natural number concepts are is to consider the performance of the chimpanzee named "Ai" (Biro & Matsuzawa, 1999; Kawai & Matsuzawa, 2000; Matsuzawa, 1985, 1996). For over 20 years, Ai has been involved in hundreds of experiments probing not only her natural cognitive ability but her cognitive potential once trained. Some of the training has focused on production and comprehension of symbols for kinds of objects, properties, and numbers. She has learned remarkably well: presented with symbols for "two,"

"red," and "pencil," Ai reliably points to an image of two red pencils. Her pattern of learning number words, however, departs strikingly from that of children. At the start of her number word training, Ai was taught the Arabic symbols for "one" and "two." Once she had learned these symbols and a new symbol for "three" introduced, Ai applied the symbols for "two" and "three" indiscriminately to arrays of two or three objects. In the initial training, Ai evidently interpreted "1" as "one" and "2" as "more than one," as do young children. Ai eventually learned to apply "2" and "3" correctly, but the amount of training needed to make this incremental advance was no different than the amount of training needed for the first two integers. When the symbol "4" was introduced, Ai's performance fell to chance on "3"; she evidently interpreted "3" as "more than two". This pattern of learning continued throughout Ai's number symbol training: she never developed a "learning set" for number and never came to interpret a new Arabic numeral as symbolizing a new cardinal value. Although human children arrive at correct interpretations of all number words after learning the first three or four of them, Ai has not progressed beyond the symbol "9" after 20 years of training. This stagnation suggests that the chimpanzees' understanding of the integers is based on a mechanism that is very different from that of human children. Chimpanzees such as Ai learn the integer list by brute association, mapping each symbol to a discrete quantity. Human children, in contrast, learn by making an induction from a limited body of evidence. Children induce that the integer list is created by a successor function, and this function generates an infinite list of numbers.

Because human infants and non-human animals lack natural number concepts, one might think that studies of these populations could not inform us about the nature of these concepts and the cognitive processes of children and adults who form and use them. We believe the opposite is the case. Children construct natural number concepts by drawing on two systems of core knowledge of numerosity: a system for representing the approximate cardinal values of large sets of objects or events, and a system for representing the exact number of object arrays or events with very small numbers of entities. These systems are spontaneously present and functional in both untrained non-human primates and in human infants. Moreover, human adults draw on the same two systems when they use natural number concepts. Comparative and developmental studies answer crucial questions about the nature of these core knowledge systems. We next review the main insights that they have yielded.

2.a. The large approximate number system

When human adults are presented with a large number of objects in a short period of time, they are unable to determine exactly how many dots are in the array without verbal counting. Under these conditions, however, adults do represent the approximate number of elements in the array. Evidence for this ability comes from three kinds of experiments. First, if adults are asked to estimate how many elements are in an array, their estimates are non-random: the mean estimated number rises linearly with increasing numerosity, and the variance of their estimate is proportional to numerosity (Whalen, Gallistel & Gelman, 1999; Cordes, Gelman & Gallistel, 2002). Second, if adults are asked to judge which of two dot arrays has more elements, their judgments are above chance, and accuracy varies with the ratio of the two numerosities: better accuracy for larger ratio differences (Barth, Kanwisher & Spelke, 2003; van Oeffelen & Vos, 1982). Findings from these experiments suggest that adults form representations of large, approximate numerosities and that their representations accord with Weber's Law: the variability in a numerosity representation is proportional to the numerosity (Dehaene, 1997, 2003; Gallistel, 1990).

Further experiments shed light on the nature of adults' numerosity representations. First, adults can perform numerical estimations and numerical comparisons on arrays of various types, including sequences of actions (Cordes, Gelman, & Gallistel, 2002; Whalen, Gallistel, & Gelman, 1999), sequences of sounds and light flashes, and visual-spatial arrays (Barth, 2001; Barth, Kanwisher, & Spelke, 2003). Second, adults can compare two numerosities as accurately when the elements in the two sets are presented in different modalities [auditory vs. visual] and formats [spatial vs. temporal] as when the elements in the two sets are the same in modality and format (Barth, 2001; Barth et al., 2003). Third, adults can perform non-symbolic arithmetic on approximate number representations of either two successive arrays of dots or one array of dots and one sequence of sounds; for example, they can mentally add the two numerosities and compare the sum to a third dot array or sound sequence. Non-symbolic addition is almost as accurate as numerical comparison, and cross-modal addition is every bit as accurate as addition within a single modality (Barth et al., in review). These findings provide evidence that adults can form, and operate on, a remarkably abstract representation of approximate numerical magnitudes. What are the phylogenetic and ontogenetic origins of this capacity? Is there a parallel signature both within and across species?

The first insights into the large approximate system of number representation came from studies of animal timing. One approach, involving operant conditioning with rats and pigeons, is called the peak procedure. On some proportion of trials, a key is illuminated and if the subject contacts the key after some fixed period of time, a food reward is delivered. On the remaining proportion of unrewarded trials, the key is illuminated for a significantly longer and variable period of time. Contacting the key after the fixed latency period for reward serves no purpose as no reward will be forthcoming. The relevant data come from these unrewarded trials. There is a peak in responding centered around the fixed latency period. For example, if the latency for reward is 20 seconds, subjects tend to contact the key for approximately 20 seconds, plus or minus a few seconds. Importantly, the variability in response is proportional to the length of the latency period. With shorter latencies, subjects respond with high accuracy and little error around the target latency; with longer latencies the distribution around the target spreads out, revealing a higher error rate. This aspect of duration representations is called *scalar variability*. The interesting aspect of scalar variability with respect to the current chapter is that the same data emerge when the task involves number as opposed to time or latency. If the subject has to make contact with the key after some number of light flashes, or some other numbered event or action, the distribution of errors is proportional to numerosity. A classic example of such data is plotted in Figure 1 (Platt & Johnson, 1971).

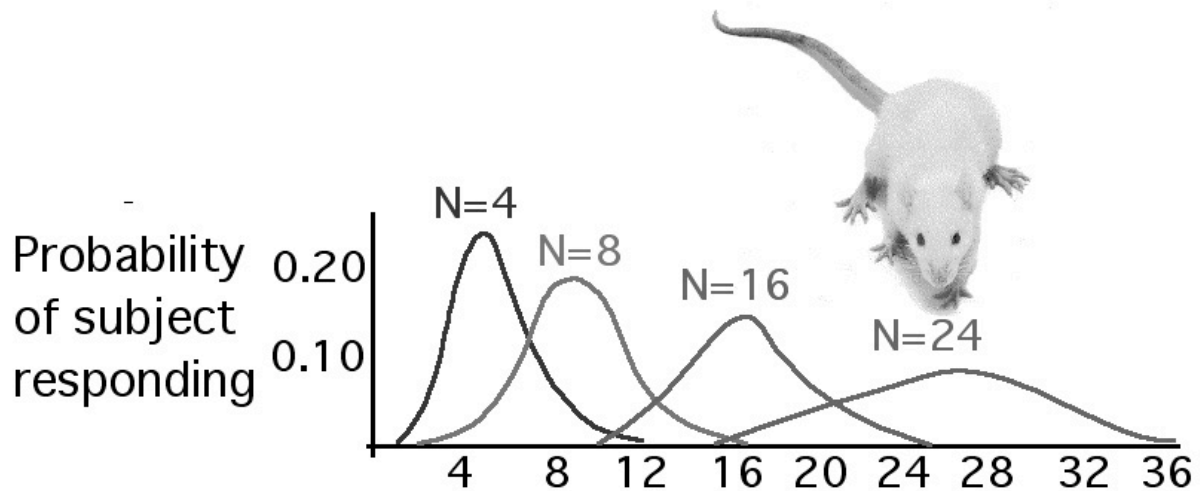


Figure 1. Plots of the probability of rats trying to access the feeding area as a function of the number of presses on a response lever and the number [N] required to load the feeding area with food; the data have been replotted from Platt and Johnson [1971].

These results, plus many others that control for factors that might explain subjects' responses other than number [e.g., effort, motivation, non-numerical stimulus dimensions: (Brannon & Terrace, 1998, 2000; Orlov, Yakoviev, Hochstein, & Zohary, 2000; Roberts, Coughlin, & Roberts, 2000)], provide evidence that trained rats, pigeons, rhesus macaques and other animals are sensitive to the approximate number of relevant events in a sequence or objects in an array (Brannon & Terrace, 2001; Gallistel, 1990; Hauser, 2000; Shettleworth, 1998). Additional data reveal that subjects' discrimination is guided by Weber's law, such that the difficulty of any given numerical discrimination depends on the ratio of the two numerosities [e.g., 8 and 12 are just as discriminable as 16 and 24, and more discriminable than 8 and 10]. Moreover, the same Weber ratio appears to characterize discrimination of the numerosities of different types of entities: objects, tones, light flashes, and self-generated actions. The Weber ratio limit is one important signature of this system of representation. The lack of modality and format effects, which suggests that the system for representing numerosity is quite abstract, is a second signature property.

A different approach to assessing the large approximate system in animals comes from training apes, like Ai, to represent and use symbols for cardinal values (Beran, 2001; Beran & Rumbaugh, 2001; Boysen & Bernston, 1989; Matsuzawa, 1985). Once Ai learned the nine Arabic numerals, she was presented with a subset of the symbols in varying spatial positions on a monitor and was taught to touch the symbols in order of ascending numerosity. Results showed that she responded faster to symbols for lower numerosities than to symbols for higher ones, and when the ordinal distance between successive numbers was large than when it was small. These effects show the classic Weber signature of the large, approximate number system. In a different series of experiments, also focused on ordinality and serial position, Ai was presented with between three to five different numbers, with spatial position varying between trials. As soon as Ai pressed the first number in the ordinal sequence, white squares covered the remaining numbers, and Ai was required to recall not only the sequence of numbers, but their location. Ai made more errors and responded more slowly when the two numbers were close together than when they were far apart. Thus, even though Ai was trained with Arabic numerals, her

performance and that of chimpanzees similarly tested (Beran & Rumbaugh, 2001; Boysen, 1997; Boysen & Bernston, 1989), show the Weber signature of the large number system.

In spite of the wealth of evidence for large, approximate number representations in non-human animals, the existence and nature of these representations has been little studied in human infants and children. For decades, studies of number representation in human infants focused only on exact discrimination of the smallest numerosities [see below]. Recently, however, investigators have begun to ask whether human infants are capable of forming the large, approximate numerical representations that are ubiquitous in non-human animals. The answer is a clear yes, even though all of the animal studies cited above involve training, while none of the studies with human infants do.

In one series of studies (Xu & Spelke, 2000), 6-month-old infants were presented with visual arrays of 8 or 16 dots [Figure 2]. On a succession of habituation trials, the sizes and locations of dots varied but the number was constant: 8 for half the infants and 16 for the others. After looking time at the arrays had declined to half its initial level, infants were tested with new arrays presenting 8 or 16 dots in alternation. To assure that any response to the test arrays was based on number as opposed to other continuous variables, the arrays with the two numerosities were equated in summed area and image size during habituation and were equated in item size and density at test; in a further study, the arrays were equated in contour length instead of summed area. Infants looked longer at the arrays presenting the change in numerosity, thereby providing evidence for numerosity discrimination (Brannon, 2002; Xu & Spelke, 2000);

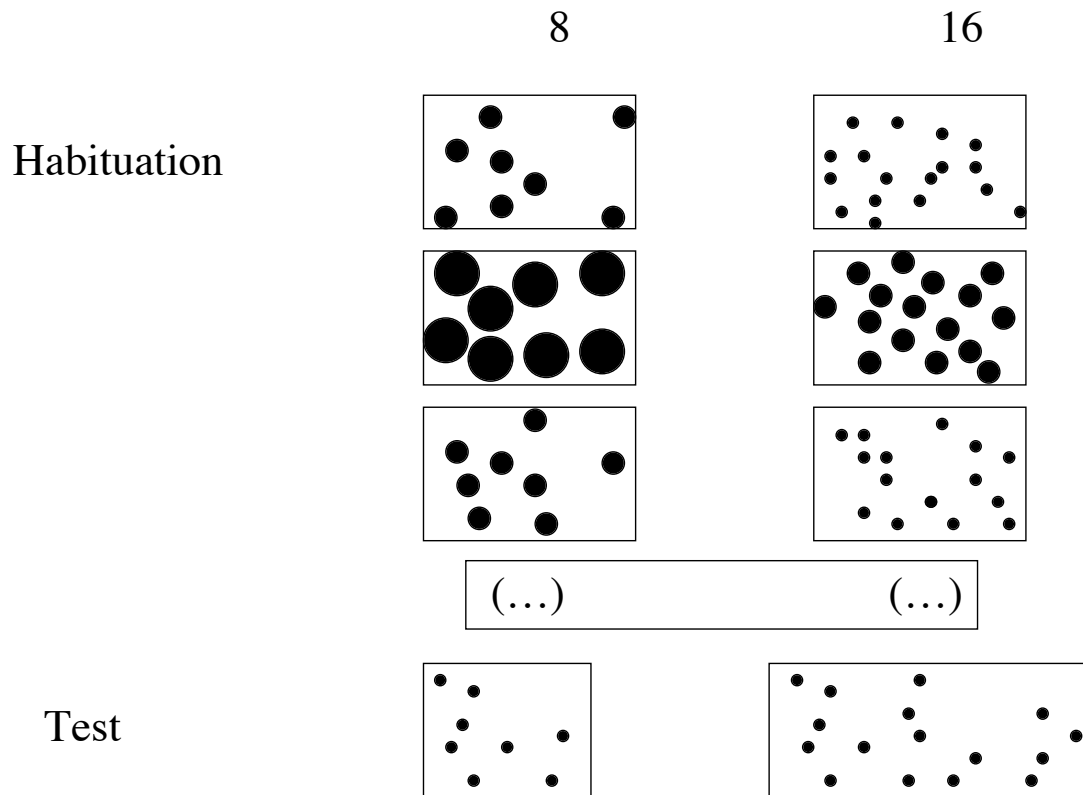


Figure 2. A sample of displays for the habituation and test phases of an experiment on

human infant number discrimination. These examples illustrate some of the variation between displays, designed to control for continuous covariates of number [e.g., continuous extent, density, etc]. Redrawn from Xu and Spelke (2000).

Further studies tested whether infants' numerosity discrimination shows the Weber signature found in human adults and in non-human animals. At 6 months, infants successfully discriminated arrays in a 2:1 ratio [4 vs. 8, 8 vs. 16, and 16 vs. 32] and failed to discriminate arrays in a 3:2 ratio [4 vs. 6, 8 vs. 12, and 16 vs. 24] (Xu, in press; Xu, Spelke, & Goddard, in review). At 9 months, infants successfully discriminated the latter arrays (Xu & Arriaga, in review). These studies provide evidence that numerosity discrimination is characterized by the Weber signature at both ages, and that the critical discrimination ratio narrows with age.

Still further studies investigated infants' numerosity discrimination with sound sequences, using a head-turn preference procedure (Kemler Nelson et al., 1995). In one study (Lipton & Spelke, in press), 6-month-old infants were presented with sequences of 8 vs. 16 natural sounds. On each familiarization trial, the quality and duration of the sounds varied but the number was constant. Then infants were tested with new sequences of 8 vs. 16 sounds. To distinguish responses to number from responses to sequence duration, sound duration, sequence rate, or correlated variables such as the amount of sound, sequences were equated for sound duration and rate during familiarization and for sequence duration and total amount of sound during the test. Infants turned their heads for longer durations when the sequences with the novel numerosity were presented, again providing evidence for numerosity discrimination.

Tests for the set size ratio signature revealed three interesting findings. First, infants again showed this signature in their discrimination of sound sequences. Second, infants showed the same developmental change in sensitivity, with a decrease in the threshold ratio from 2.0 to 1.5 between 6 and 9 months. Third, infants showed exactly the same pattern of success and failure when tested with auditory temporal sequences as they had shown when tested with visual spatial arrays. The latter finding suggests that numerosity discrimination in infants shows a second signature of the system found in animals: It depends on an abstract process that is independent of sensory modality [visual or auditory] and stimulus mode [spatial vs. temporal].

As pointed out above, the studies of infants differ from those of animals in that infants represent number spontaneously, with no training. These findings raise the question whether untrained animals also represent numerosity under the conditions used with infants, if such representations also show the Weber signature of the large approximate number system, and if so, whether the ratio thresholds are the same or different. To address this issue, an experiment was designed (Hauser, Tsao, Garcia, & Spelke, 2003) with cotton-top tamarin monkeys using the same stimulus controls and same general methods as in the work with human infants (Lipton & Spelke, in press); the only significant methodological differences were in the use of speech syllables for the tamarins and in the implementation of a familiarization-discrimination procedure. As in previous work on tamarins with this method (Hauser, Newport, & Aslin, 2001; Ramus, Hauser, Miller, Morris, & Mehler, 2000), we measured whether the subject turned in the direction of a concealed speaker when each test sequence was played. If subjects had extracted the common number of syllables from the familiarization phase of the session, then in the test phase they were expected to respond more to the tokens with a different number of syllables than to the tokens with the same number of syllables. Results provide clear evidence of the large approximate number system, with successful discrimination at ratios of 2:1 and 3:2, but not 5:4 [Figure 3].

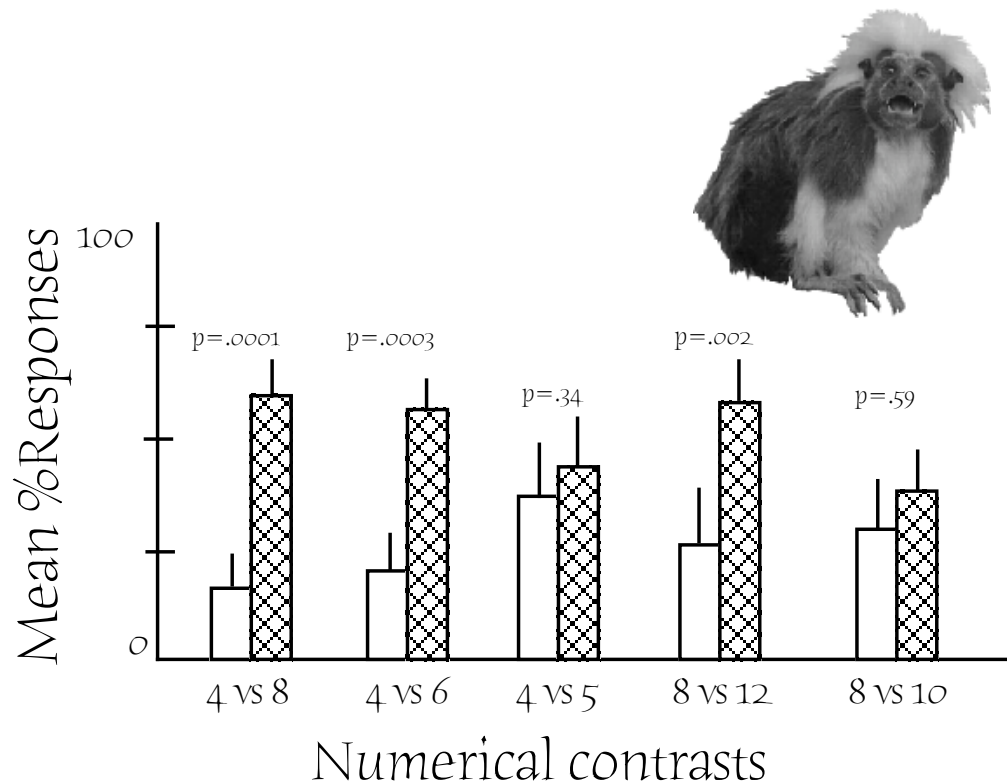


Figure 3. Results from familiarization-discrimination experiments on cotton-top tamarins. The y-axis plots the mean proportion of responses [i.e., head orienting to a concealed speaker] to test items [speech syllables] with either the same [white bars] or different [cross-hatched bars] numbers as the familiarization sequence. P-values are for Wilcoxon-signed ranks tests. Redrawn from Hauser et al. [2003].

Finally, very recent research has begun to ask what computations young children perform on large, approximate numerosities. In studies of young children (Barth et al., in review) there is evidence that subjects can add two different numerosities. For example, children watch as one array of blue dots appears and then disappears behind an occluder; then a second array of blue dots appears and disappears behind the same occluder. Finally, children are presented with an array of red dots and are asked whether there are more blue or red dots. When tested with ratio differences of 1.75, 1.67, and 1.5 between the comparison dot array and the sum of the first two arrays, children performed well above chance, suggesting that this kind of representation can enter into computations of addition (Barth et al., in review; Lamont, Barth, & Spelke, 2003). Recent studies of adult rhesus monkeys have begun to address similar issues of addition operations over large approximate numerosities (Flombaum, 2002; Flombaum, Junge, & Hauser, in prep).

In summary, studies of trained animals, untrained animals, human infants, and preschool children all provide evidence for a core system of number representation. This system serves to represent the approximate cardinal values of large sets of objects or events with two well-established signatures, and evidence for a third underway. First, it is subject to a Weber limit on discrimination—discriminability depends on the set size ratio. Second, it is characterized by a common discrimination limit across modalities. The third signature concerns mathematical operations that take approximate mental magnitudes as input.

We now consider evidence for a second core system of number representation. The

mechanisms underlying this system differ from the large approximate system, and so do its limits.

2.b. The small precise number system

For more than a century, psychologists have recognized that there is something special about very small numbers. When human adults are asked to enumerate the exact number of elements in a visual array of dots, their response time rises linearly with increasing numerosity for all integers greater than 3. With the numbers 1-3, however, response times are fast and nearly flat. Although the nature and interpretation of this reaction time function has been much debated (Balakrishnan & Ashby, 1992), subjects' ability to identify small numbers rapidly, coupled with their introspections, suggests that a parallel process underlies enumeration of the smallest sets. Psychologists christened this pre-attentive, unconscious process "subitizing" (Butterworth, 1999; Mandler & Shebo, 1982).

Research over the last decade has revealed that this subitizing process has four signature properties. First, as noted above, it is subject to a set size limit of 3 or 4. Second, it operates when elements occupy distinct spatial positions but not when they are superimposed or embedded within one another (Trick & Pylyshyn, 1994). Third, it operates when distinct elements are separated by empty space but not when they are joined by a grid of connecting lines (Scholl & Pylyshyn, 1999; Trick & Pylyshyn, 1994). Fourth, it operates when elements are stationary, when they move continuously while remaining in view, and when they move continuously with periods of brief occlusion; it fails to operate when elements appear and disappear discontinuously (Scholl & Pylyshyn, 1999) or when elements disperse and coalesce (Mitroff, Scholl, & Wynn, in review; Scholl, 2001). Scholl and Pylyshyn have proposed that subitizing depends on mechanisms of object-directed attention: mechanisms that allow human adults to track 3-4 objects in parallel, provided that the objects are cohesive, bounded and move continuously.

Over the past two decades, a wealth of experiments provide evidence that this system of representation is shared by human infants. Wynn's (Wynn, 1992) celebrated study of "addition and subtraction" serves as an example. In one version of Wynn's experiment, 5-month-old infants viewed a puppet stage containing one object [a Mickey Mouse doll], and then the object was hidden behind a screen. Then a second, featurally identical object entered the scene and moved behind the same screen. To assess whether the infants had represented exactly two objects behind the screen, Wynn used the expectancy-violation method briefly mentioned in the last section: she raised the screen to reveal either the correct number of objects [two] or an incorrect number [one]. Even though infants had only seen a single object on the stage at any given time, they looked longer at the one-object array. This looking pattern provides evidence that infants tracked each of the two objects over occlusion and formed a representation of both objects behind the screen. In subsequent versions of this study, infants were found to take correct account both of the addition and the subtraction of an object, in arrays of as many as three objects. When shown larger numbers of objects, infants failed Wynn's task, looking equally long at possible and impossible outcomes.

Subsequent research reveals that Wynn's findings are highly robust, for they have been obtained from converging experiments using two other methods. In a box-search method (Feigenson & Carey, in press), 10 and 12-month-old infants watched as two objects were placed into a box, one at a time [1+1] and then one of the objects surreptitiously removed. Then the infants were allowed to reach into the box and retrieve one object, and finally their subsequent

reaching into the box was measured. In this condition, infants spent considerable time reaching back into the box. In contrast, they spent reliably less time reaching into the box if they initially saw only one object placed in the box, or if they were given the chance to remove two objects. This pattern of performance provides converging evidence that infants are capable of representing exactly two objects. In subsequent variations, infants were found to represent up to 3 objects. They failed this test, however, when larger numbers were presented, even larger numbers that differ by a large ratio.

The final method involves a two-box choice discrimination task (Feigenson, Carey, & Hauser, 2002). Here, an experimenter first presented infants with two widely separated boxes, placed different numbers of cookies into each box, walked away and then allowed the infants to crawl to either of the boxes. Infants crawled reliably to the box with the greater number of cookies, provided that neither box contained more than three cookies. When larger numbers of cookies were placed in one or both boxes, in contrast, infants failed to show a preference in their approach patterns [Figure 4]

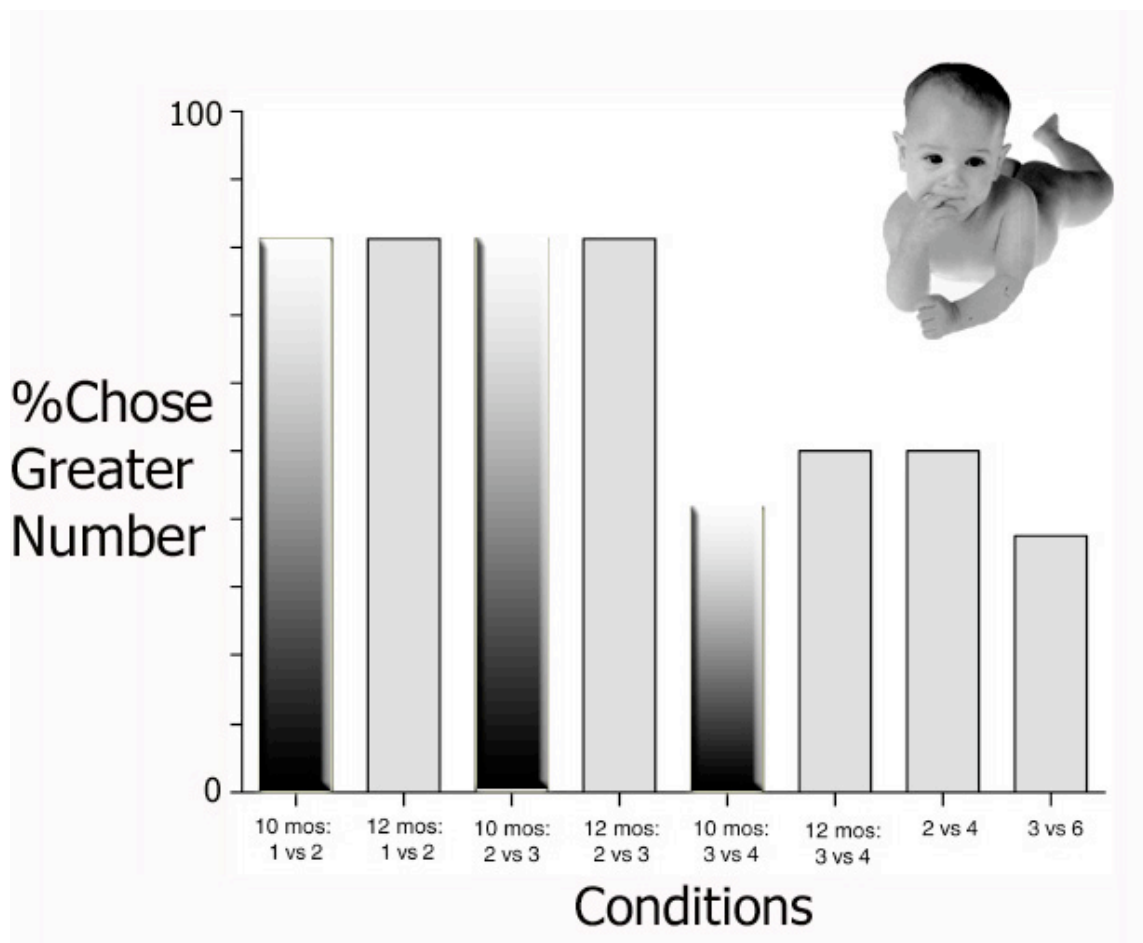


Figure 4. 10 and 12-month old infants responses in a 2-box choice test. The y-axis plots the proportion of subjects choosing the box with the greater number of cookies, and the x-axis plots the conditions by age of subject. Redrawn from Feigenson et al. [2002].

The above findings show that [a] infants' small-number representations have the set size signature of adults' subitizing, and [b] infants' small-number representations do *not* have the

Weber signature of large number representations. Further studies of object representations in infants provide evidence for the other signatures of the adult object-tracking system as well (Mitroff et al., in review; Scholl, 2001; Scholl & Pylyshyn, 1999; Spelke, 2000). These findings suggest that a system for representing small numbers of objects is common to infants and adults, and that it is distinct from the system for representing large numbers of objects.

Evidence for the small exact number system in animals comes from the same methods used with human infants. The first experiment on animals to employ the looking time method involved a replication of Wynn's (Wynn, 1992) addition and subtraction experiments focusing on a population of semi-free ranging rhesus monkeys (Hauser, MacNeilage, & Ware, 1996). Monkeys were tested on Wynn's $1+1 = 2$ vs 1 task and her $2-1 = 1$ vs 2 task. There were four primary differences with Wynn's design. In contrast to Wynn, and most other studies with human infants, the rhesus experiments used [i] a between subjects design, [ii] no or minimal familiarization trials, [iii] an experimenter in view, and [iv] eggplants as test objects. In addition, since the rhesus live on an island, subjects were free-ranging with many potential distractions around the testing area. Despite these differences, analyses of both conditions revealed striking parallels with subjects looking longer in both addition and subtraction conditions at the impossible event. In subsequent experiments, monkeys succeeded on the further tasks of $1 + 1 = 2$ or 3 , 1 small + 1 small = 1 big or 2 small, $2 + 1 = 2$ or 3 and $2 + 1 = 3$ or 4 (Hauser & Carey, in press); they failed, however, when the outcome numbers exceeded three [e.g., $2+2 = 3$ vs 4 vs 5] or when the number of times the representation required updating in short term working memory was greater than two [see Figure 5 below]. The $1+1 = 1$ vs 2 vs 3 findings were replicated with captive cotton-top tamarins using a within subject design (Uller, Hauser, & Carey, 2001), as well as with domesticated dogs (West & Young, 2002).

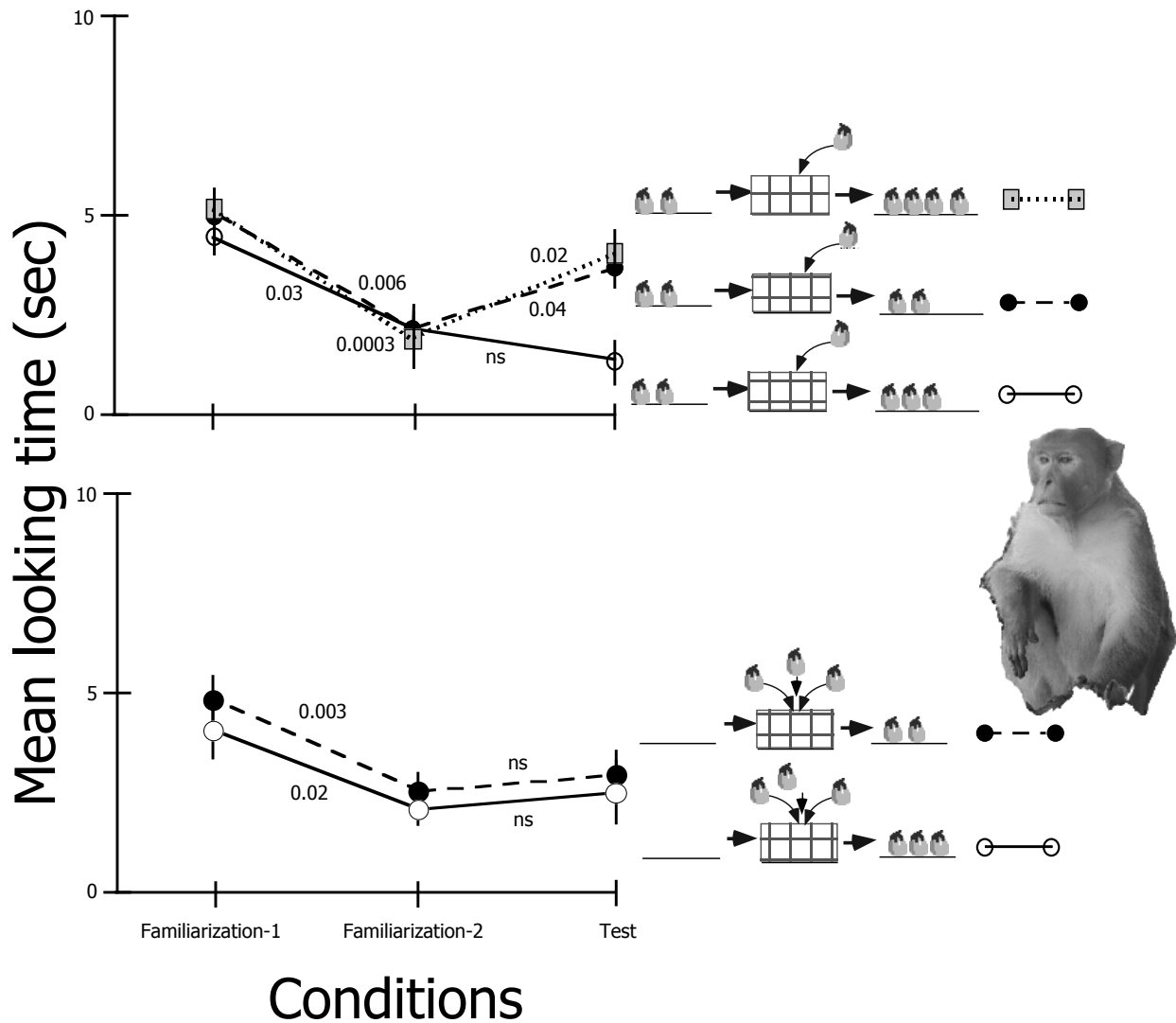


Figure 5. Looking time studies on rhesus illustrating updating problem for $2+1 = 2$ vs 3 vs 4 and $1+1+1 = 2$ vs 3 . The y-axis plots the mean amount of time [seconds] looking at the two familiarization trials and one test trial. Redrawn from Hauser and Carey [in press].

To further explore the limits on animal's spontaneous number capacity, Hauser and colleagues used the box search (Santos, Sulkowski, Spaepen, & Hauser, 2002) and the two-box discrimination (Hauser, Carey, & Hauser, 2000) methods used with infants². For both experiments, each subject was tested in only a single trial, thus eliminating any effects of experience or training. In the two-box discrimination task, an experimenter located a lone rhesus monkey and in the initial experiments, presented two empty boxes subsequently placed approximately one meter apart on the ground. Each box was then loaded up with different numbers of apple pieces, controlling for side and order of placement. Rhesus selectively approached the box with the larger quantity for 2 vs 1 , 3 vs 2 , 4 vs 3 , and 5 vs 3 .

² Of historical interest, though most of the spontaneous methods used in animals were first implemented with human infants, the two-box discrimination task was first developed for rhesus monkeys and then used by Feigenson and colleagues [2002] with human infants.

Rhesus might solve the two-box discrimination task by timing the events as opposed to counting the number of objects placed into each box. They might also solve this problem by quantifying volume as opposed to the number of pieces of apple. To address the time versus number confound, Hauser and colleagues reran all of the initial contrasts but this time equated number of objects placed into each box by using a rock. In other words, when rhesus were presented with a comparison of 2 pieces of apple versus 1 piece of apple, the total number of objects was equated by placing a rock into the box with 1 piece of apple. Under these conditions, rhesus continued to pick the larger quantity in 2 vs 1, 3 vs 2, and 4 vs 3. To address the possibility that rhesus attend to volume over number, Hauser and colleagues placed 3 pieces of apple in one box and 1 piece of apple equal in volume to the three in the other box. Here again, subjects picked the box with 3 pieces of apple over the box with one piece.

A subsequent series of experiments involved the same general logic, but this time explored subtraction as opposed to addition (Sulkowski & Hauser, 2000). In the prototypical setup, subjects were shown two empty platforms, and then some number of objects were placed onto each, sequentially. An occluder was then placed in front of each platform, blocking the subject's view. The experimenter then reached down and removed some number of objects from one or both platforms. Independently of the particular setup or the number of objects removed, the rhesus successfully picked the platform with more objects with all quantity pairs involving 3 or fewer objects. Thus, if one platform had three plums and the other had two plums and a rock, and the experimenter removed one plum from each, subjects approached the platform with 2 plums over the platform with 1 plum.

These two-box choice experiments suggest that rhesus can compute additions and subtractions over discrete objects, and for the addition experiments can discriminate the number of objects placed into each box when the ratio is 4:3. These conditions do not yet allow us to distinguish between the small and large systems. To distinguish between these systems, contrasts with larger numbers are needed. In subsequent conditions, Hauser and colleagues tested rhesus on 8 vs 4 and 8 vs 3, ratios that fall well within those discriminated for smaller numbers. Rhesus failed each of these conditions; their lack of discrimination can not be accounted for by inattention as only subjects who attended to the entire presentation were included in the final data set. These failures suggest that rhesus engage the small exact number system when tested in the two-box discrimination method. If the large approximate system had been available and engaged, they would have performed as well on 2 vs 1 as 8 vs 4.

In summary, the system used by human adults to apprehend small, exact numerosities is present and functional both in human infants and in two species of non-human primate. These findings suggest that this system is both ontogenetically and phylogenetically primitive. It is a second core system of numerical representation.

3. Putting the systems together

We have argued that human adults, adult non-human primates, and human infants share two capacities for numerical representation, one allowing approximate representations of large sets of entities and a second allowing exact representations of small numbers of objects. Because the performance of all these populations shows the same signature limits—especially the ratio limit of large number representations and the set size limit of small number representations, we suggest that these numerical representations depend on mechanisms that are homologous across monkeys, apes and humans and that are constant over human development. What, however, do these claims, and the evidence that they are based on, tell us about the uniquely human capacities for constructing the natural numbers? We hypothesize that humans depart

from their closest living primate relatives by using these two systems in ontogeny to make sense of number words and the counting routine. Even after humans acquire the capacity to enumerate sets by counting, however, they retain the two core systems and use them during all quantitative reasoning tasks.

The two core systems found in infants and monkeys help to make sense of preschool children's otherwise puzzling interpretations of number words and the difficulty they experience in understanding verbal counting. When children first engage in the verbal counting routine, they know only that "one" picks out a single object, and that the other number words pick out larger sets of objects. At this stage, children may map "one" to their representations of objects and they may map the other number words to their representations of large approximate numerosities. When, over the next 1-2 years, children learn the meanings of the words "two" and "three," they may map each of these terms to two representations at once: a representation of an array of objects ["two" refers to an array with an object and another object and no other objects] and a representation of an approximate numerosity ["two" refers to a very small set]. Once children have learned these terms, they are in a position to notice that the progression from "two" to "three" in the counting routine corresponds both to the addition of one object to the set and to the increase in the cardinal value of the set. These inductions could form the basis for all the natural number concepts.

This account makes a set of predictions that can be tested with human adults, and if confirmed, would explain both how children construct this system and why nonhuman animals will never do so regardless of training. If children construct the natural number concepts by using natural language—number words and verbal counting—to link together core representations of small exact and large approximate numerosities, then the natural number concepts of adults may depend on three systems: the two core systems and natural language. Research has begun to test these predictions, with some success. In particular, adults given tasks that require representations of the natural numbers have been found to activate representations of large, approximate numerosities (Dehaene, 1997), and neurological patients with impaired abilities to form large, approximate number representations show impairments in natural number representations and mental arithmetic (Lemer, Dehaene, Spelke, & Cohen, in press). These findings suggest that the core system for representing large, approximate numerosities partially underpins uniquely human natural number concepts. Moreover, adults who perform mental arithmetic on exact or approximate large numerosities show greater activation of language areas of the brain in the former case, and bilingual adults who learn new facts about large exact numbers are better able to access that information in the language in which it was learned; in contrast, bilinguals who learn new facts about large, approximate numbers or small exact numbers are equally able to retrieve the facts in their two languages (Dehaene, Spelke, Pinel, Stanescu, & Tsivkin, 1999; Spelke & Tsivkin, 2001). These findings suggest that natural language is involved in the representation of uniquely human natural number concepts, but that language does not influence the approximate number representations that human adults share with infants and with non-human primates.

4. EvoDevo approaches to core knowledge

We have focused on number because it is one of the most comprehensively studied cognitive systems. The topic of numerical knowledge has been explored from both a phylogenetic and developmental perspective, using the tools of ethology, developmental psychology, cognitive science, neurobiology, linguistics and anthropology. The Nobel laureate Nikolaas Tinbergen (Tinbergen, 1963) suggested almost fifty years ago that a comprehensive

analysis of a particular behavior will require answers to four different questions: 1] What is its phylogenetic or historical background? 2] What is its original adaptive function? 3] What neurophysiological mechanisms are responsible for its expression? 4] How does it develop from its initial to the mature state? We have addressed each of these questions except the second. At present, we have little understanding of the adaptive pressures that led to either the shared core systems or the uniquely human system of the natural number concepts. Animals clearly benefit from quantifying small numbers precisely, as occurs when they form coalitions, when mothers track the number of offspring present, or when individuals engage in reciprocal exchanges (Gallistel, 1990; Hauser, 2000; Lyon, 2003). Animals also may benefit from the large approximate system during foraging and inter-group aggression. But these are claims concerning current utility as opposed to original function. When it comes to our uniquely human capacities such as verbal counting and natural number operations, our understanding of the relevant selective pressures is even less. Both our numerical and linguistic knowledge systems appear to rely on a generative mechanism to create a limitless range of meaningful expressions (Hauser, Chomsky, & Fitch, 2002), it is not clear whether one mechanism evolved first for language and then for number or whether two distinct mechanisms evolved separately (Bloom, 1994; Corballis, 1992, 1994). Further phylogenetic and ontogenetic studies may help to shed light on these questions. For example, several small scale societies such as the Hadza of Tanzania and the Piraha of Brazil have words for the first few integers and then use the equivalent of "many" for all other quantities (Butterworth, 1999; Dehaene, 1997; Gordon, in review) These people have a fully expressive language that is based on the power of generativity, but they appear to lack a system of natural number concepts, relying exclusively on the small precise and large approximate systems (Gordon, in review). Detailed anthropological studies of such cultures may help pinpoint some of the functional benefits of this system, as well as the social and ecological pressures that led to its emergence.

The framework outlined here, and applied specifically to numerical knowledge, has direct implications for cognitive neuroscientists interested in the cellular mechanisms that support the two core systems. As reviewed elsewhere in this volume [see chapter by Piazza & Dehaene], two recent studies with macaques provide exquisite evidence for a neural signature of the large approximate system, with one study using a self-generated motor response (Sawamura, Shima, & Tanji, 2002) and the other using discrimination of static visual arrays (Nieder, Freedman, & Miller, 2002). Both studies entailed massive amounts of training prior to testing the subjects on their behavioral discrimination of different numerosities. If the trained macaques have an abstract representation of number, however, they should be capable of spontaneously transferring from one input modality to another and of performing numerical operations such as addition. To shed light on these numerical representations and operations, it would be highly desirable for neurophysiological studies to begin to employ the techniques currently being used by behaviorally oriented primatologists, reviewed above, to explore the spontaneously available resources for numerical discrimination.

Behind these specific suggestions is a more general one. When human adults form and use concepts that no other animal can attain, they do so by assembling a set of building blocks that are shared with other animals. These building blocks are part of core knowledge. Language may be a powerful device for assembling and coordinating the systems of core knowledge. Studies of non-linguistic animals and prelinguistic infants, however, are uniquely placed to tell us what those systems are, how they evolved, and how they unfold over ontogeny.

5. References

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