# Evolutionary and developmental foundations of human knowledge

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## I. 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. 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. Without them we wouldn't be able to learn about different kinds of games, mathematics, cooking, or maps. 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 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, the system is relatively automatic and impervious to explicitly held beliefs and goals[1].

In this chapter, we use the domain of number to illustrate how core knowledge systems are assembled to permit uniquely human cognitive advances. We consider first two lines of research that elucidate core knowledge systems: comparative evolutionary studies and studies of human development. These studies provide evidence for two core knowledge systems that

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[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.

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. Then we consider how children use these systems to construct the first uniquely human number concepts: the natural numbers. Finally, we consider 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.

# II. Comparative evolutionary approaches

Consider the following apocalyptic scenario. You are an alien scientist from another planet and you descend to earth to find only one species: *Homo sapiens*. You are interested in why this species looks and behaves as it does, as well as why it has the kind of social organization observed. How might you find answers to these functional problems? Since you are an atheist alien, you sweep aside explanations of divine cause. What you turn to instead is an exploration of evolutionary design, of trying to understand the relationship between the trait's engineering and the kind of problem it appears to solve (Dawkins, 1986; Williams, 1966). Having read Darwin, you might conclude that only natural selection can account for a trait with complex design features — an assemblage of parts with a nonrandom probability of developing together. But there is a deep problem with this approach. Although you might find out something about current function, you will never know whether this represents its original function; nor will you understand whether the now extinct inhabitants of earth, including all of the direct and indirect predecessors of *Homo sapiens*, had similar qualities; and neither will you understand whether the observed trait represents the only solution to the problem at hand. Finding fossils of other species will help explain anatomical traits, but will only lead to speculation about behavior, psychological representation, and neural instantiation. You, the alien scientist, are stuck.

Fortunately, we have not yet witnessed this apocalyptic scenario. Nature has left us with a treasure trove of species, some closely related and some distant. In this section, we lay out the general logic of comparative studies in order to motivate an evolutionary approach to understanding conceptual knowledge in humans; though we acknowledge that comparative studies should, can, and often do focus on a wide range of species that excludes humans, we concentrate here on comparisons between human and nonhuman primates because we are particularly interested in explaining the evolutionary and ontogenetic origins of our own conceptual systems; we further acknowledge that many of the capacities that are present in nonhuman primates may also be present in non-primate animals. We first detail some of the central questions in comparative studies, and show why they are essential for cognitive neuroscientists. We then discuss some of the different approaches to these questions, emphasizing several new directions that bear on problems of knowledge and its underlying neural foundation.

There are three essential questions in the sciences of the human mind that either necessitate a comparative approach, or are greatly enriched by it:

1. *Is the trait in question unique to humans?*
2. *Does the acquisition of the trait depend upon particularly human capacities?*
3. *What functional problem does the trait in question solve, and did it evolve for this particular function?*

Let us unpack each of these questions to clarify the scope of the problem. Claims of uniqueness are inherently claims that can only be checked by comparative data. Comparative data are needed to determine whether humans are the only species with a given behavioral capacity, such as a capacity to recognize faces, use tools, or represent exact numerosities. If the comparative data reveal that at least one other species expresses the trait in question, then further comparative data are needed to determine whether the trait is a *homology* or a *homoplasy*. For example, face recognition abilities would be shown to be homologous in humans and monkeys if they depended on the same mechanisms: mechanisms that presumably evolved in a common ancestor of these primates. Face recognition abilities would be shown to be homoplastic if they depended on distinct mechanisms: mechanisms that presumably evolved independently in the two lineages.

Comparative cognitive neuroscientists distinguish homologous from homoplastic mechanisms by discovering the behavioral and neural *signatures* of a mechanism in one species and then testing for those signatures in other species. For example, both the neural and psychological mechanisms underlying face processing in humans show a number of behavioral signatures, including degradation when faces are inverted, and neural signatures, including spatially localized cortical activations. The same signatures have been found in monkeys tested in face recognition tasks, providing evidence that the mechanisms of face recognition are largely homologous in human and nonhuman primates (Gross & Sergent, 1992; Kanwisher, Downing, Epstein, & Kourtzi, 2001; Kanwisher, McDermott, & Chun, 1997; Perrett et al., 1988; Perrett et al., 1984; Rolls, 2000; Tarr & Gauthier, 2000). In contrast, both the neural and psychological mechanisms underlying the acquisition of species-typical vocalizations show different signatures in humans, nonhuman primates and Passerine songbirds. For example, in both humans and in songbirds, but in neither monkeys nor apes, young are capable of imitating the sounds produced by adults. Thus, vocal imitation is a behavioral signature in humans and songbirds, one classified as a homoplasy due to its absence in nonhuman primates. Similarly, the capacity for vocal learning is mediated by a set of discrete and dedicated neural circuits in both songbirds and humans, but with no evidence for comparable circuitry in the nonhuman primates (Doupe & Kuhl, 1999; Doupe, Brainard, & Hessler, 2000; Hauser, 1996; Jusczyk, 1997; Nottebohm, 1999; Pinker, 1994; Seyfarth & Cheney, 1999).

The second question concerns the extent to which the emergence of one cognitive faculty depends on the emergence of another. For example, consider the capacity to attribute mental states to others — to have a "theory of mind" (Premack, 1986; Premack & Premack, 2002; Premack & Woodruff, 1978; Wimmer & Perner, 1983). We can ask whether this capacity depends on the acquisition of language by investigating mentalistic reasoning in pre-linguistic human infants and in patients with selective damage to the language faculty. If theory of mind is found in these populations, however, it still might depend on prior evolutionary constraints on brain development that are linked to language, because these humans are equipped with brains that evolved the capacity to acquire language. A stronger test of the independence of mentalistic reasoning and language would come from studies of animals (Cheney & Seyfarth, 1990; Hauser, 2000; Povinelli, 2000; Premack & Premack, 2002; Tomasello & Call, 1997) who, based on most accounts, lack several of the key computational capacities that allow for the expressive power of human language (Hauser, Chomsky, & Fitch, 2002). Recent evidence from chimpanzees suggests that in the absence of training, and with the use of a competitive task, individuals readily use the perceptual act of seeing to make inferences about the mentalistic capacity of knowing (Hare, Call, Agnetta, & Tomasello, 2000; Hare, Call, & Tomasello, 2001). Although the proper interpretation of these findings is still debated (Povinelli & Vonk, 2003; Tomasello, Call, & Hare, 2003), they begin to suggest that a core capacity for mentalistic reasoning emerged in evolution prior to, and independently of, the emergence of the language faculty.

The third question sets up a distinction between the problem of original function and current utility. In the absence of robust comparative data on different species, it is impossible to ascertain with certainty that a particular cognitive ability in humans was specifically designed for its current function. Take, for example, the capacity in language to create a limitless scope of meaningful expressions by recombining a discrete set of elements. Did this mechanism evolve for communication in particular? It is difficult to come up with a data set that rules out alternative functions. For example, this mechanism also plays a role in our internal dialog, in mathematics, and possibly, in social relationships and spatial navigation. Comparative data can play a key role here. Assume that chimpanzees fail to use a generative mechanism in their communicative expressions, but implement this kind of mechanism in number computation. This pattern would suggest that the capacity for generativity evolved for number and was then coopted in human evolution for language and communication; although it is possible that this capacity evolved independently in these two lineages, this seems like the least likely scenario given our evolutionary proximity to chimpanzees.

Not all cognitive neuroscientists are compelled by these evolutionary questions. Even those who are not, however, should appreciate that comparative data are centrally useful for specifying the nature and architectural relations among the mechanisms that give rise to human mental life. Animal studies can shed special light on human cognitive function in three ways. First, as noted above, study of animals can serve to reveal what cognitive capacities are inherently connected and what capacities are relatively independent. When humans are found to have cognitive systems A and B, and a non-human animal is found to have system A' [with signatures indicating that it is homologous to A] but not B, we may conclude that B was not necessary for the evolution, ontogenetic development, or mature functioning of A. Second, the neural mechanisms of mental function can be studied by invasive methods in animals that are ethically not possible with humans, provided that the mental functions of the model animal are homologous to those of humans. For example, consider the significant amount of work conducted on fear responding and amygdala function in rats, macaques, and humans. Both rats and monkeys have also been used as models for understanding autism (Adolphs, Tranel, Damasio, & Damasio, 1995; Amaral & Corbett, 2002; Bachevalier, 1994; Ingram, Tisdale, & Rodier, 1995; LeDoux, 1996; Rodier, 1996). In the case of fear, both species have an emotion that we call "fear" with both physiological and behavioral signatures that parallel those observed in humans. It is also clear, however, that the phenomenology — what it's like to feel fear — is most likely very different in humans and other animals (Kagan, 1998). Invasive studies of rats and monkeys therefore may shed light on some, but not other, aspects of humans' fear response. The same line of reasoning applies with even greater force to comparative studies of autism as neither rats nor monkeys normally have a theory of mind — they are naturally mind blind.

A third, essential role for animal studies, is in titrating and controlling the level and kind of experience provided to a developing animal. Much of what is known about the contributions of maturation and visual experience to the development of visual perception comes from such controlled rearing studies. Classic examples include Hubel and Wiesel's studies of the effects of binocular deprivation on the development of binocular function in cats and monkeys, and Gibson and Walk's studies of the effects of dark rearing on the emergence of visually guided locomotion [e.g., Walk, Gibson & Tighe, ref]. Further studies of experiential effects focus not on systematic deprivation of input but on systematic variation in the types of inputs given to animals. For many captive animals, for example, we not only know the precise kinds of experience they have had during development, but we can selectively give or withhold certain experiences that have no bearing on proper development. For example, consider the observation that human infants, by the age of eight months, can compute transitional probabilities between successive events that occur repeatedly in a continuous stream: a computation that may play a role in segmenting the continuous stream of speech into meaningful units such as words (Saffran, Aslin, & Newport, 1996). We can next ask whether other species are capable of similar computations (Hauser, Newport, & Aslin, 2001), and if so, whether this ability requires certain kinds and amounts of prior experience.

Once the comparative approach is adopted, further questions arise. First, what are the most appropriate species for comparison with humans? Answers to this question depend on a proper understanding of each species' capacities and the extent to which the research focus requires evidence at the level of homologies or homoplasies. Second, what are the most appropriate testing environments and testing methods? One important distinction here is between training procedures that provide exceptional control over the stimulus conditions and spontaneous methods that enable an assessment of what species do "naturally", thereby providing a more direct route into its evolved function. Although we recognize the value of training procedures, we focus here primarily on spontaneous methods, because these provide the most direct parallels with studies of human infants, they promise greater insight into adaptive function, and they provide a new set of tools[2] for cognitive neuroscientists interested in the neurophysiology of animal cognition and behavior.

# III. Developmental approaches

If anything is clear to the most casual observer, it is that human infants are supremely incompetent beings. At birth, infants see with low resolution, move with little coordination, accomplish almost nothing by their own actions, say not a word, and don't appear to understand that other individuals have a rich mental life filled with beliefs and desires that often differ from their own. Moreover, the period of human infancy and early childhood is a time of prodigious developmental change. Over the space of a few short years, children learn to identify the people around them and to anticipate their actions, to categorize objects into an encyclopedia of artifacts with canonical functions, to master the phonology, lexicon, morphology, syntax and semantics of their native language [or languages, for the many children living in multilingual environments], to figure out the layout of significant places in their environment and the most efficient routes between them, to gain crucial motor skills, and to appreciate that other humans often share the same beliefs, sometimes have different ones, and with such knowledge, monumental feats of deception are possible. How can we characterize these changes, and the brain and cognitive systems that make them possible?

The last half-century of research has provided us with numerous means to study the capacities of incompetent infants and to compare the capacities of children of different ages (Carey, 1985; Gopnik & Meltzoff, 1997; Keil, 1989; Kellman & Arterberry, 2000; E. S. Spelke & Newport, 1998). This research revealed first that infants are endowed with a host of perceptual capacities, including mechanisms for discriminating speech sounds and parsing utterances into syllables and words, mechanisms for perceiving depth and using depth information to guide

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[2] One of the advantages of spontaneous methods is that experiments can be run quickly, especially when contrasted with the often time consuming efforts required for training monkeys in visual or auditory discriminations. One drawback of these methods for neuroscientists, however, is that they require relatively large sample sizes, a luxury that neurophysiological experiments with primates often lack.

spatially appropriate actions, and mechanisms for parsing the surface layout into objects. More recent research has revealed that such infants also have capacities to represent and reason about more abstract properties of the world, including the difference between animate and inanimate objects, the relationship between self-propelled motion and intentional actions, and numerosity, the focus of our specific case study. Much of this evidence suggests that infants' cognitive capacities are continuous with those of adults.

How do developmental psychologists discover whether the capacities of infants and adults are continuous or discontinuous? One cannot read continuity or discontinuity off the behavior of children in a simple way. Much relies on the mapping between behavior and underlying psychological or neural mechanism. For example, children aged 2, 3, and 4 years may all appear to behave similarly when shown an array of objects and asked "How many?": all will point to the objects in succession and produce the verbal count list. Recent experiments provide evidence, however, that younger children's understanding of these actions is profoundly differently from older children: only the oldest children understand that the words of the counting routine refer to numerosities and that the routine itself functions to enumerate the items. In humans of different ages, as in animals of different species, similarity of behavior does not in itself imply commonality of mechanism.

Developmental psychology also provides many examples where dissimilarity of behavior need not imply difference of mechanism. For example, infants aged 8, 12, and 18 months show profound differences in their patterns of search for hidden objects. Recent experiments provide a wealth of converging evidence, however, that a common mechanism for representing small numbers of objects underlies the performance of infants at all these ages; we describe this mechanism, and the evidence for it, below.

How then can psychologists and neuroscientists discover the true developmental continuities and discontinuities in cognitive mechanisms? Here the logic used in evolutionary studies suggests a direct analogy: One compares the behavioral signatures of cognitive capacities in infants, children and adults. If the same signature characteristics and limits are observed at different ages, then those common signatures provide evidence for a common system of core knowledge at work at the different ages. From such evidence, one can then probe further, using modern neuroimaging techniques (ERP, fMRI) to assess whether common neural signatures are observed when children of different ages are tested under the same conditions. With such evidence in hand, one can then take the further step of comparing the neural systems recruited in humans at different stages of development with the systems recruited by nonhuman primates. And once our understanding of the underlying genetic mechanisms are better understood, one can take the final step of comparing molecular commonalities and differences. A recent glimmer of such evidence comes from studies of speech production and the finding that the FOXP2 gene complex is recently evolved and unique to our species (Enard et al., 2002).

A positive example in which common signatures provide evidence for common mechanisms, comes from Held's classic studies of the development of stereopsis in infants [ref]. Human infants begin to discriminate displays with no disparity from displays with crossed or uncrossed disparities at about 16 weeks of age. Does this ability reflect the development of mature mechanisms of stereopsis? To address this question, Held focused on three signatures of stereopsis in human adults: hyperacuity [stereoacuity in excess of grating acuity], sensitivity to horizontal disparities only, and sensitivity to disparities only within a critical range. At the first moment when infants began to respond to stereo displays, they showed all three of these signatures. Despite vast quantitative changes in acuity over the course of infancy and early childhood, these signatures provide evidence for a common mechanism of stereo vision.

A negative example, in which differing signatures provide evidence for distinct mechanisms, comes from recent studies of developing representations of food objects. Five-year-old children categorize food objects primarily by their substance properties rather than by their form (Macario, 1991) as do adult rhesus monkeys (Macario, 1991; Santos, Hauser, & Spelke, 2001). When children are shown that a given food object tastes good, they generalize their learning to other objects with the same color and texture irrespective of shape. When children are shown two food objects that touch each other, moreover, they use color and texture differences to specify the boundary between them (Xu & Carey, 1996); rhesus monkeys show a parallel pattern (Munakata, Santos, O'Reilly, Hauser, & Spelke, 2000; Xu & Carey, 1996). Human infants also learn about food objects, but they fail to show these signature patterns. Infants generalize learning about food objects by shape as much as by color and texture [Shutts, in prep]. Moreover, infants fail to parse food objects at color/texture boundaries [Condry et al., ref]. These findings suggest that domain-specific representations of food objects emerge between the first and the fifth year of age; at present, however, we have little understanding of the mechanisms that change or the experiences that are necessary for such change.

In the cases discussed, studies of young children shed light on the emergence of adults' capacities. When adults are found to exhibit a capacity that young children lack, however, such studies serve a further purpose: Like studies of animals, they can reveal the building block systems that give rise to the adult's capacities. Representation of food objects again serves as an example. Although very young children do not categorize solid food objects by their colors and textures, they do categorize non-solid food substances by these properties [Shutts & Goldvarg, ref]. This finding raises the possibility that representations of non-solid substances provide a foundation for children's learning about food objects. Current research, testing young children's generalization of learning about non-solid and solid objects, is testing this hypothesis.

Our case-study of number development provides another, more worked out example of how studies of early development shed light on the building blocks of mature cognitive capacities. We focus on our capacity for number not only because the empirical evidence for its ontogeny is rich, but because there is equally substantial evidence for the principles underlying numerical competence in the adult state [see chapter by Piazza & Dehaene], how the brain represents such knowledge, and how such systems evolved from an ancestor that long predates the origin of our own species. In fact, number may represent the best worked out system of core knowledge to date, with well developed theoretical models, and detailed empirical work in humans and animals that cuts across the levels of behavior, mind, and brain.

# IV. Knowledge of number: A test case

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. Even the most highly trained chimpanzees and 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 6 toy fish reliably will typically only know 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 — 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 insist that the pile still contains "four fish" [Condry et al., 2002]. 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 related to not only her natural cognitive ability but her cognitive potential once trained. Some of the training has involved the capacity to produce and comprehend 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, differs 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, she did not spontaneously generalize with the introduction of a new symbol for "three". Instead, 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." With further training, Ai learned to apply "2" and "3" correctly, but the amount of training needed to make this incremental move 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; note that there are at least two ways in which she might have drawn this inference, either by considering the new symbol to represent the next integer in the count sequence or some other number greater than the last integer learned. Because she never drew this inference, Ai's required the same amount of training or more to learn the remaining numbers in the integer count list. Although human children figure out how counting works without training, and 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 is not due to experimenter fatigue, but rather, the realization that the chimpanzees' understanding of the integers is based on a mechanism that is wildly 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 [training is unnecessary] and functional in both 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. Here we review the main insights that they have yielded.

## IV.a. Representations of large, approximate numerosities

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 experiments of three sorts. First, if adults are asked to estimate how many elements are in the 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 (Lipton & Spelke, 2002, in press; Van Oeffelen & Vos, 1982). 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. To give a sense of these findings, the reader is invited to run a mock version of this experiment in Figure X below. For the first experiment, quickly look and look away at the figure on the left and then write down the number of dots. For the second experiment, quickly look and look away at the figure on the right and then write down whether the figure on the left has more or less dots than the one on the right. Most of you probably answered something like 20 for the figure on the left, with the correct number of dots equal to 19. Most of you probably also answered that the figure on the right has more dots than the figure on the left which is correct; the figure on the right has 24 dots. Findings from these two experiments suggest that adults form representations of large, approximate numerosities and that their representations accord with Weber's Law (Dehaene, 1997, 2003; Gallistel, 1990): the variability in a numerosity representation is proportional to the numerosity.

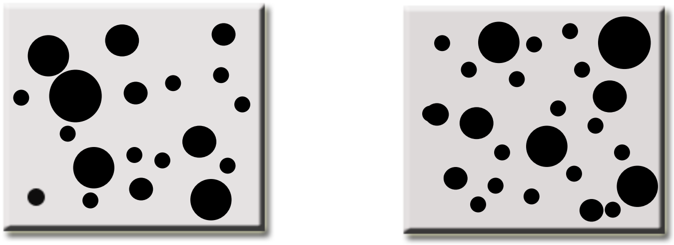

Figure X. A display of randomly placed dots used in experiments on rapid number estimation. If you quickly look and then look away at the figure on the left, you should be able to give an approximate estimation of the number of dots; the actual number is 19. If you then quickly look and look away at the figure on the right, you should be able to say which of these two figures has more dots; the figure on the right has 24 dots.

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, as well as 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: when presented with two successive arrays of dots [as in Figure X above], 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, Dehaene, LaMont, Lipton, Kanwisher & Spelke., submitted]. 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 below, redrawn from work by Platt and Johnson (Platt & Johnson, 1971).

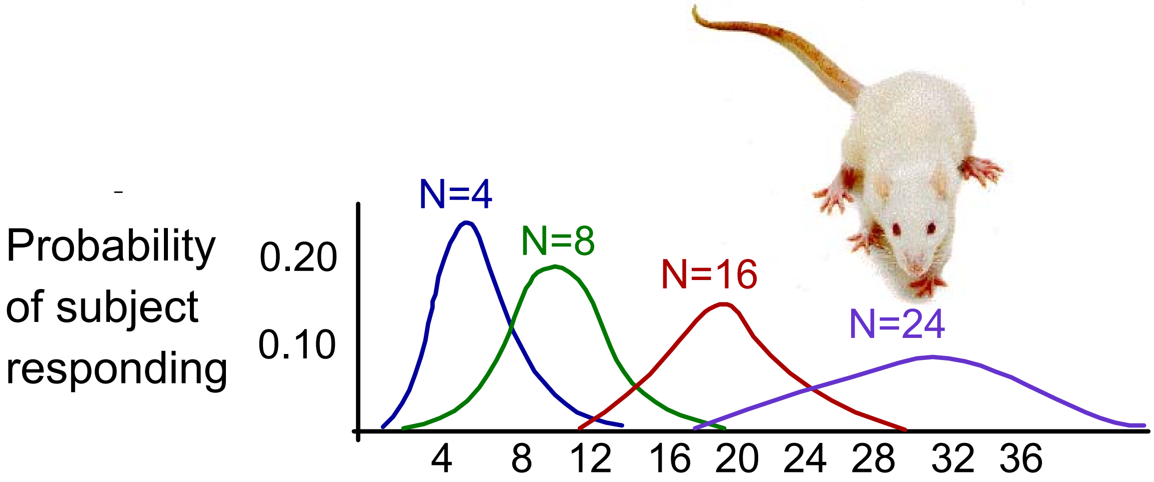

Figure X. Plots of the probability of rats trying to access the feeding area as a function of the number of presses on a response lever and the number (N) required to load the feeding area with food (Platt & Johnson, 1971).

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 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 on a monitor, 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. As revealed below [Figure X], 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.

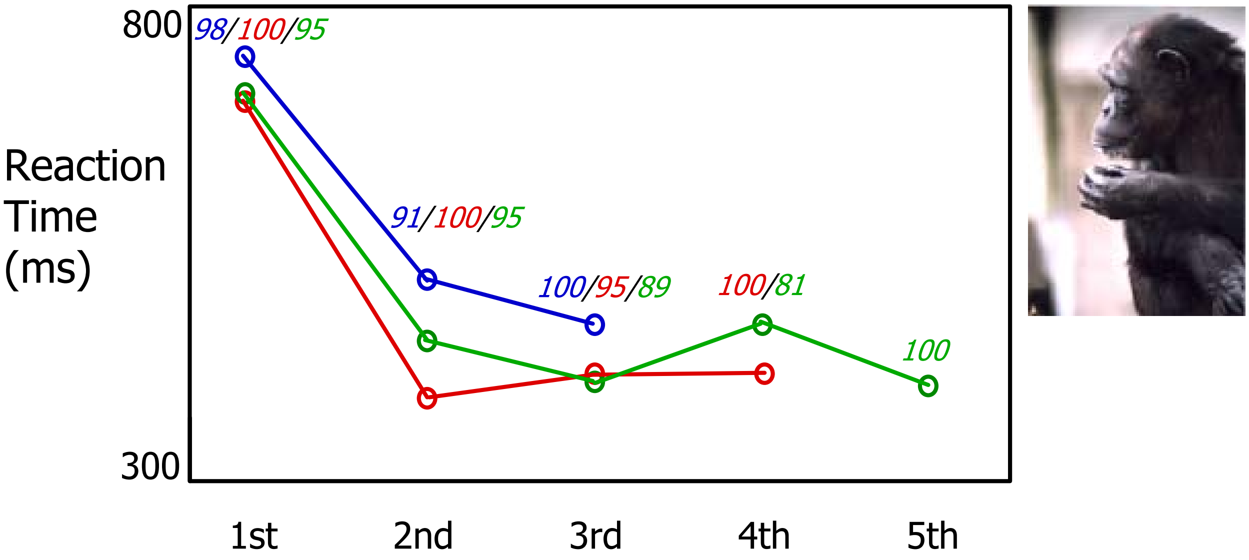

Figure X. Ai's response to a serial order task involving Arabic numerals. The y-axis plots reaction times [milliseconds], the x-axis the ordinal position of the number presented on the monitor. Blue symbols refer to 3-item lists, red to 4-item lists, and green to 5-item lists. Above each cluster of points are data on percent correct with respect to contacting the correct number in the ordinal sequence.

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, 6-month-old infants were presented with visual arrays of 8 or 16 dots [Figure X]. 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 X.

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 et al., in prep]. At 9 months, infants successfully discriminated the latter arrays [Xu & Arriaga, in preparation]. 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 [Jusczyk et al., date]. In one study, 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 [see Figure X]. 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 with cotton-top tamarin monkeys using the same stimulus controls and methods as in the work with human infants (Lipton & Spelke, in press). Individual tamarins were placed in a sound proof test chamber and familiarized with multiple tokens of different speech syllables [e.g., MO, SA, TU]. During familiarization, subjects passively listened to tokens of a particular target number [depending upon the experiment, this varied between 4 to 12 repetitions of the same syllable], systematically manipulated to vary along the dimensions of syllable type and duration, inter-syllable duration, total signal energy, and speaker's voice pitch and gender. Thus, if a subject was familiarized on the number four, it would hear strings such as MO-MO-MO-MO, SA-SA-SA-SA, and TU-TU-TU-TU spoken by male and female speakers, and with syllable/inter-syllable duration varying. Consequently, the only common element in the familiarization set was number. The test trials consisted of new syllable types of both the same and different number as for the familiarizations [e.g., in a 4 vs 6 comparison, subjects would hear PI-PI-PI-PI vs PI-PI-PI-PI-PI-PI, as well as other syllables]. The range of syllable and inter-syllable durations, as well as the gender and pitch of the speaker's voice in these test trial stimuli, were chosen such that only number could be used as a discriminative cue. As in previous work on tamarins with this method (Hauser et al., 2001; Ramus, Hauser, Miller, Morris,

& Mehler, 2000), we measured whether the monkey turned in the direction of a concealed speaker located 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 of 2:1 and 3:2, but not 5:4 [Figure X]. Preliminary evidence suggests that this discrimination may extend down to 2 vs 3 (Hauser, Dehaene, Dehaene-Lambertz, & Patalano, 2002; Hauser, Garcia, & Spelke, unpublished data); if discrimination extends down to the smaller numbers, then the underlying mechanism is importantly different from that exhibited by human infants.

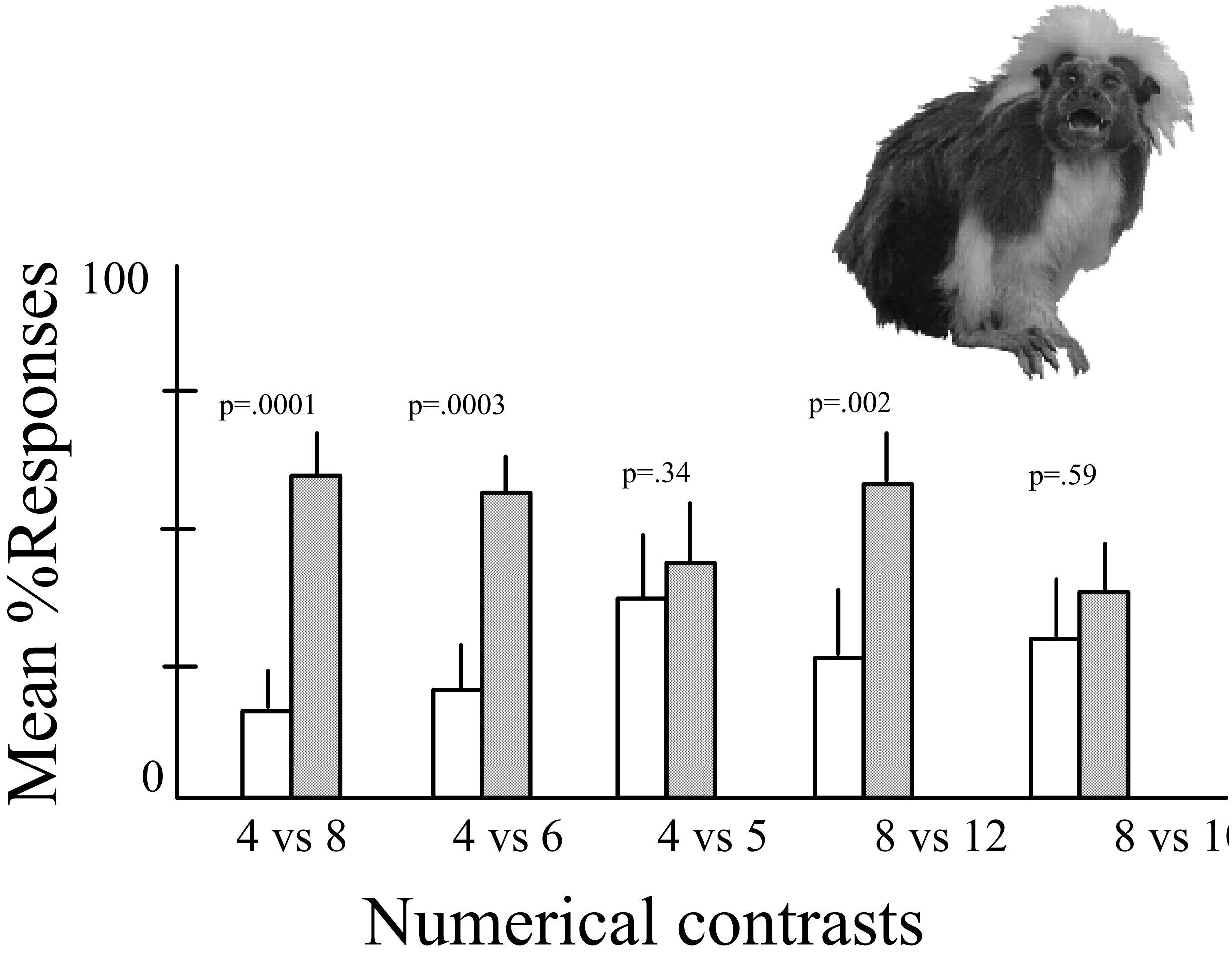

Figure X. Results from hab-dishab with speech syllables providing evidence of mental magnitudes.

Finally, very recent research has begun to ask what computations animals and young children perform on large, approximate numerosities. In studies of young children [Barth et al., submitted] and adult rhesus monkeys (Flombaum, 2002; Flombaum, Junge, & Hauser, in prep), there is evidence that subjects can add two different numerosities. For example, children watch as one array of blue dots appear and then disappear behind an occluder; then a second array of blue dots appear and disappear behind the same occluder. Finally, they are presented with an array of red dots and are asked to say whether there are more blue or red dots. When tested with a ratio difference of 3. 5 between the dot arrays, children performed well above chance, suggesting that this kind of representation can enter into computations of addition. In studies of adult rhesus monkeys, subjects are tested on the violation of expectancy looking time procedure that has been used with infants and monkeys [see below for complete description]. In brief, the logic is that if subjects detect a physically impossible event, they will look longer than if the event is possible. Each subject watched as different numbers of objects were first placed behind a screen and then the screen removed to reveal the correct or incorrect outcome. Rhesus monkeys looked longer at the impossible outcome in contrasts involving 3+1 = 4 vs 8, 2+2 = 4 vs 8, 4+4 = 4 vs 8; rhesus failed to show a difference in looking time when the operation was 2+2 = 4 vs 6.

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, and it has two well established signatures, with evidence for a third underway. First, it is subject to a Weber limit on discrimination—discriminability depends on 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.

## IV.b. Representations of small exact numerosities

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 numbers of 4 and above [Figure X]. 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" [e.g. 19th c ref., 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 imbedded 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, but it fails to operate when elements appear and disappear discontinuously (Scholl & Pylyshyn, 1999) or when elements disperse and coalesce [Scholl, date]. 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 and 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 (, 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, 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 [Figure X]. 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. Infants failed Wynn's task, looking equally long at possible and impossible outcomes, when shown larger numbers of objects.

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 watch as two objects are placed into a box, one at a time [1+1] and then one of the objects is surreptitiously removed. Then the infants are allowed to reach into the box and retrieve one object, and finally their subsequent reaching into the box is measured. In this condition, infants spend considerable time reaching back into the box. In contrast, they spend 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 fail this test, however, when larger numbers are presented, even larger numbers that differ by a large ratio [Figure X].

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

The above findings clearly 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 [see Scholl, date & Spelke, 2000, for discussion]. 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 (Hauser, MacNeilage, & Ware, 1996) focusing on a population of semi-free ranging rhesus monkeys. 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 lived 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 fact, the effects were much larger than in infant studies, with the duration of looking to the impossible test condition approximately equal to the first familiarization trial and almost twice as long as to the possible test condition. 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). The 1+1 = 1 vs 2 vs 3 findings were replicated both with captive cotton-top tamarins using a within subject design (Uller, Hauser, & Carey, 2001), as well as domesticated dogs (West & Young, 2002).

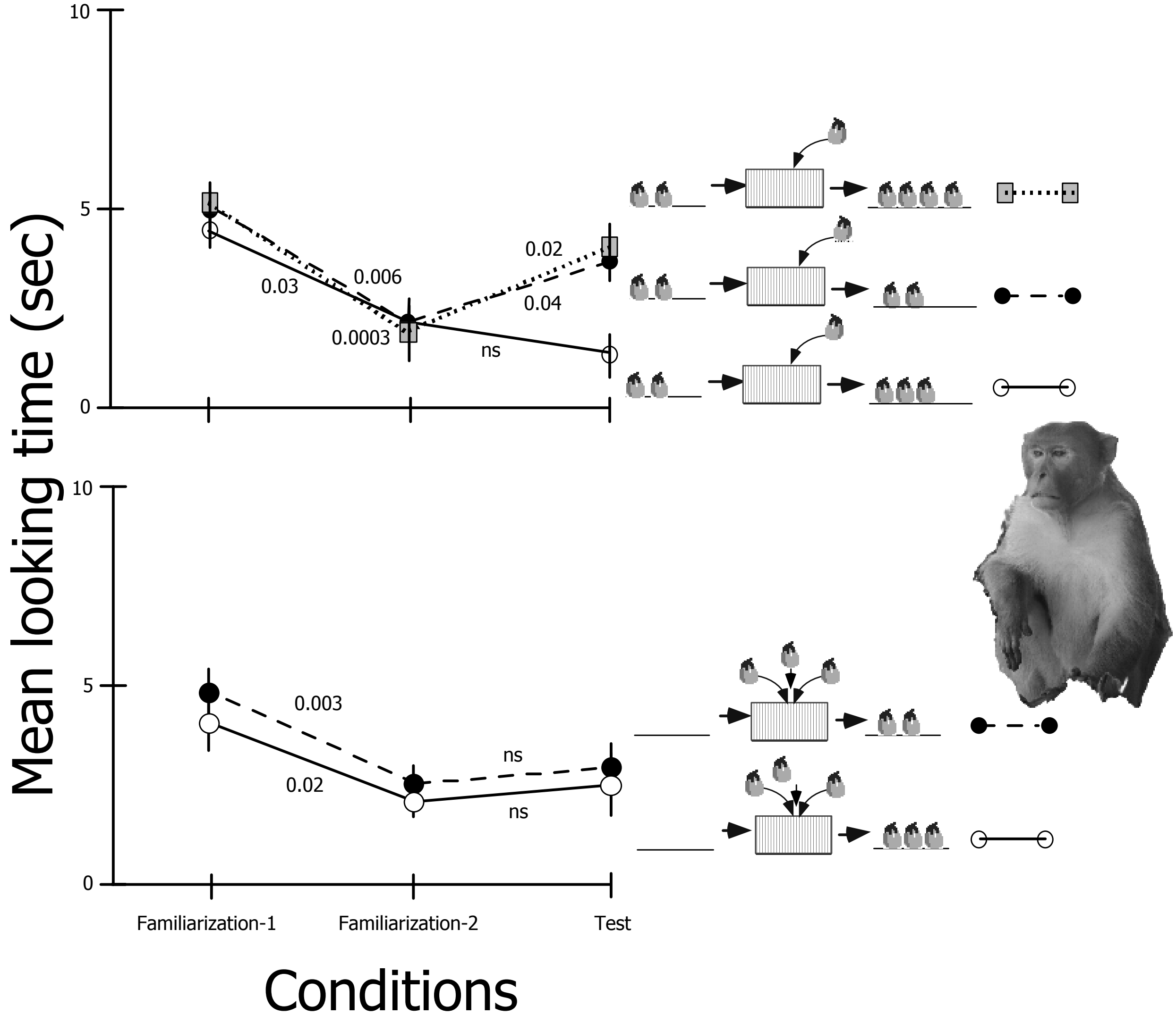

Figure X. Looking time studies from rhesus illustrating updating problem for 2+1 = 2 vs 3 vs 4 and 1+1+1 = 2 vs 3.

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 infants[3]. 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. In the initial condition, the experimenter then showed one piece of apple and placed it into one box, showed one rock and placed it into the other box, and then walked away giving the subject an opportunity to approach. Consistently, subjects approached the box with the apple. This simple condition shows that subjects attend to the experimenter, watch where the objects are placed, recall their location, and selectively approach food over a rock. Using this method, and controlling for order of placement and side, subsequent conditions showed that individual rhesus selectively approached the box with the larger quantity for 2 vs 1, 3 vs 2, 4 vs 3, and 5 vs 3.

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. At present, it is unclear why rhesus succeed on a looking time version with the same ratio and absolute

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[3] 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 with human infants.

numbers [i.e., 2:1 and 4 vs 8], but differences in the task demands are one possibility [see Tables 1 and 2].

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.

# V. Putting the systems together

We have argued that human adults, adult non-human primates, and human infants share two systems of numerical representation. Because of humans' evolutionary proximity to the monkeys and apes, we further argue that these systems are homologous. 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. Once humans acquire this novel capacity, however, they nonetheless to tap the two core systems during quantitative reasoning tasks that prevent verbal counting.

The two core systems found in infants and monkeys help to make sense of preschool children's otherwise puzzling interpretations of number words and verbal counting. When children first learn 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.

Although no direct evidence bears on this account, it 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, submitted]. 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 the natural numbers, but that language does not influence the number representations that human adults share with infants and with non-human primates.

# VI. 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 (, 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 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 (Hauser, 2000). They also benefit from the large approximate system, a mechanism that is presumably tapped 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 capacity, our understanding of the relevant selective pressures is even less. For example, given that both our numerical and linguistic knowledge systems rely on a generative mechanism to create a limitless range of meaningful expressions (Hauser, Chomsky, & Fitch, 2002), it is not at all clear whether this mechanism evolved first for number or first for language, or whether there are two separate mechanisms (Bloom, 1994; Corballis, 1992; Corballis, 1994). Further phylogenetic and ontogenetic studies may help to shed light on the functions of core number representations, especially when those representations are elicited and used by untrained animals. For example, it appears that young children are productively stringing together words to create a variety of meaningful expressions a full year or more before they have such abilities with number words or written symbols. What is also clear, however, is that the generative capacity can be operative in one domain and not the other, even in normal, non-brain damaged adults. 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). These people have a fully expressive language that is based on the power of generativity. But they lack a large exact number system, relying exclusively on the small precise and large approximate systems. Detailed anthropological studies of human cultures that lack a verbal counting routine (Butterworth, 1999; Dehaene, 1997\ Gordon, in press), compared with cultures living in a similar state but with a verbal counting system, may help pinpoint some of the functional benefits of this system, as well as the social and ecological pressures that led to its evolution.

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 the 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, while simultaneously uncovering the neural code. Several questions emerge from this work concerning the patterns of activity that would arise in the absence of training.

Relating these two neurophysiological studies back to our earlier discussion, if the macaques trained in these experiments have an abstract representation of number, then in principle they should be capable of spontaneously transferring from one input modality to another as demonstrated in earlier studies of rats (Church & Meck, 1984). Thus, for example, the macaques trained by Sawamura and colleagues to tap out the correct number should be able to do the same and then equate this number with a sequence of auditory tones or the presentation of a comparable number of dots on a monitor. Similarly, the macaques trained by Nieder and colleagues should be able transfer their knowledge of the number of objects in a visual array to a discrimination of the number of tones or actions. To shed light on the nature of these numerical representations, however, it would be highly desirable for neurophysiological studies to begin to employ the techniques currently being used by behaviorally oriented primatologists to document the spontaneously available resources for numerical discrimination. Thus, which areas of the brain are active during violation of expectancy looking time studies involving number? Which areas are recruited during the two-box choice task or during habituation-dishabituation experiments with speech syllables? Answering these questions will not only show whether such methods provide viable alternatives to those involving training, but will showcase whether the limits of number discrimination are the same with and without training. At the same time, behavioral studies with humans would benefit from adopting some of the training methods developed and used with animals. Understanding how training influences number discrimination in nonhuman primates may have some bearing on how we think about more applied issues in mathematical education, as well as possible therapies for patients that have incurred damage to number-related circuits.

Behind these specific suggestions is a more general one. When human adults form and use concepts that no other animal can attain, we do so by assembling a set of building blocks that we share 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 they are, how they evolved, and how they unfold over ontogeny.

Table X. Studies of Number in Animals: Different methodological approaches

| Method | Stimuli | Species | References |
|---|---|---|---|
| Training: Identification of number by constructing symbol-quantity association | Visual or auditory Arabic numerals | Chimpanzees, Orangutans, African gray parrots | (Biro & Matsuzawa, 1999; Boysen & Bernston, 1989; Boysen & Berntson, 1995; Kawai & Matsuzawa, 2000; Matsuzawa, 1985, 1996; Pepperberg, 1994, 2000) |
| Training: Identification of number with varied representations controlling for non-numerical properties (e.g., volume, duration, etc.) | Static visual, auditory, actions | Rats, pigeons, rhesus macaques, chimpanzees | (Brannon & Terrace, 1998, 2000; Davis & Perusse, 1988; Fernandes & Church, 1982; Gallistel, 1990; Gallistel & Gelman, 2000; Meck & Church, 1983; Nieder, Freedman, & Miller, 2002; Olthof, Iden, & Roberts, 1997; Platt & Johnson, 1971; Rilling & McDiarmid, 1965; Roberts et al., 2000; Sawamura, Shima, & Tanji, 2002) |
| Training: Identification of number following summation of symbols or objects | Arabic numerals, food | Chimpanzees, rhesus macaques | (Beran, 2001; Beran & Rumbaugh, 2001; Boysen, 1996, 1997; Rumbaugh & Washburn, 1993; Washburn & Rumbaugh, 1991) |
| Spontaneous: Identification of number using habituation-dishabituation | Speech syllables, tones | Cotton-top tamarins | (Hauser, Dehaene et al., 2002; Hauser, Tsao, Garcia, & Spelke, in review) |
| Spontaneous: Identification of number using a looking time, expectancy violation procedure with addition and subtraction operations | Food objects | Cotton-top tamarins, rhesus macaques | (Flombaum, 2002; Hauser & Carey, 1998, in press; Hauser et al., 1996; Uller et al., 2001) |
| Spontaneous: Identification of larger number based on summation of objects added to or subtracted from a concealed area | Food objects | Rhesus macaques | (Hauser et al., 2000; Santos et al., 2002; Sulkowski & Hauser, 2000) |

## Table X. Methods and relevant parametric variables in studies of numerical abilities in human infants/children and nonhuman animals

| Method | Species | Training/ Spontaneous | Static/ Moving Display | Sequential/ Simultaneous Display | Auditory/ Visual/ Both | Subject Response | Math Operation |
|---|---|---|---|---|---|---|---|
| Expectancy violation | Human,<br>Rhesus,<br>Tamarins | S | S/M | Seq | A | Duration of looks | Add,<br>Subtract |
| Habituation-Dishabituation | Humans,<br>Tamarins | S | S/M | Seq/Sim | BM | Duration of Looks, Look | None |
| 2-box search | Humans,<br>Chimpanzees<br>Rhesus | S |  | Seq | V | Pick larger quantity | Add,<br>Subtract |
| 1-box reaching | Humans<br>Rhesus | S | M | Seq | V |  | Add |
| Trained Categorization/ Generalization | Rats,<br>Pigeons,<br>Rhesus<br>Chimpanzees | T | S | Seq/Sim |  |  |  |
| Arabic numerals | Humans<br>Chimpanzee<br>Rhesus<br>Parrot | T | S | Seq/Sim | V/A | Labeling, Pointing to symbols in ordinal sequence | Ordinal arrangements, Add |

# VI. References

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