How Evolution Constrains Human Numerical Concepts

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ABSTRACT—***The types of cognitive and neural mechanisms available to children for making concepts depend on the problems their brains evolved to solve over the past millions of years. Comparative research on numerical cognition with humans and nonhuman primates has revealed a system for quantity representation that lays the foundation for quantitative development. Nonhuman primates in particular share many human abilities to compute quantities, and are likely to exhibit evolutionary continuity with humans. While humans conceive of quantity in ways that are similar to other primates, they are unique in their capacity for symbolic counting and logic. These uniquely human constructs interact with primitive systems of numerical reasoning. In this article, I discuss how evolution shapes human numerical concepts through evolutionary constraints on human object-based perception and cognition, neural homologies among primates, and interactions between uniquely human concepts and primitive logic.***

KEYWORDS—*brain; counting; evolution*

Human infants, children, and adults can estimate numerical values without counting and with crude precision. Human infants dishabituate to changes in the numerosity of a visual set during studies of looking time (1). Young children can choose the numerically larger of two sets of objects (2). Adults can rapidly tap out the approximate number of flashes they see in a sequence while also doing a verbal distractor task (3). Across these groups and studies, participants' ability to discriminate is constrained by the numerical differences between the sets they compare. While estimating number, the fidelity of an individual's representation decreases with the magnitude of the set, which results in lower accuracy for proportionally small differences compared to large differences (4). This constraint is known as Weber's law: The ability to discriminate depends on the ratio between the quantities being compared. Even people in parts of the world where counting is not part of the language or culture can nonverbally estimate and compare numerical values from sets of objects, and obey Weber's law in their accuracy (5). The ability to estimate numerical values nonverbally is apparently universal in humans and independent of verbal counting.

In this article, I propose that number representation in humans is a result of the joint satisfaction of many evolutionary constraints on primates' perceptual and cognitive systems. I discuss four types of constraints: First, I propose that numerical reasoning provides a rational solution to a vexing problem, which is how the disparate vocabularies of distinct sensory modalities and spatiotemporal dimensions are integrated into a holistic representation of quantity in the environment. Second, I propose that the disposition of humans' quantity system to represent number, beyond other continuously varying quantitative dimensions, is driven in part by a bias in primates' perceptual systems to parse inputs into discrete objects. Third, I argue that the neural substrates of human quantitative cognition are constrained evolutionarily, which imposes functional constraints on the organization and flow of numerical information. Fourth and finally, I argue that the human symbolic counting system interfaces with these evolutionarily primitive numerical and logical operations, evidence of continued constraints on numerical cognition in modern-day humans. These four constraints operate at different levels and are not mutually exclusive; rather, they jointly constrain the basic organization of numerical processing in the human mind.

NUMBER REPRESENTATION IS A RATIONAL QUANTITATIVE STRATEGY

Despite evidence that numerical representation is widespread in humans and animals, some recent work has questioned

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whether representations of nonverbal quantity are truly numerical during infancy (6) or ever (7). The argument is that many dimensions—including spatial extent (surface area, contour), density, brightness, and duration—are correlated with number in nature and could explain behavioral and neural responses to numerosity. Infants and animals are sensitive to the correlations among those variables (8–10). However, the ability to represent correlations among number, area, time, and other dimensions does not mean that those representations are not distinct for infants or animals, just like the ability to represent a correlation between the color of the sky and the likelihood of a storm does not mean one cannot differentiate the sky and rain. Many quantitative dimensions are likely represented by infants and animals, and the mechanisms that represent each dimension could be functionally similar as a result of a common origin or algorithm (11, 12). Yet these dimensions, even if associated or correlated, may be psychologically distinct. To determine whether our species represents number as a distinct dimension, we should consider causal hypotheses about why number would be represented.

Number could be represented as a distinct dimension because it is the rational solution to quantity discrimination in the environment. Number is a quantitative dimension that can be abstracted across sensory modalities, space, and time. Many types of quantitative representations could be used to compare sets of objects, but not many of them afford the same degree of abstraction as *number*. For example, cumulative surface area, density, duration, and rate are all quantitative dimensions. However, many of these non-numerical dimensions are limited to representation by only a subset of sensory modalities; one cannot hear the cumulative surface area of a set of objects. In contrast, number is a quantitative dimension that can be represented in any sensory modality. Moreover, unlike rate (temporal) or density (spatial), a numerical sum can be calculated from sets distributed over both space and time.

Crossmodal and spatiotemporal representation of numerosity has been demonstrated in newborn human infants, children, nonhuman primates, and other animals (13, 14). The computational flexibility *number* affords could make it an optimal dimension for comparing sets of objects under natural conditions such as occlusion, interruption, and integration of sets across the senses, space, and time. This argument about the primacy of *number* in perception is supported by evidence that wild animals preferentially compare numerical values as opposed to mass or area during natural decisions (15); furthermore, in computational models of set representation, *number* emerges spontaneously and independently of density and surface area during unsupervised statistical learning of sensory input (16). Additionally, number representation may have an added advantage for primates: It is an object-based representation ideally suited to the object-based nature of primates' visual processing.

OBJECT-BASED PERCEPTION CONSTRAINS QUANTITY REPRESENTATION

Preexisting constraints on primates' perception could cause number to become a dominant dimension for representation of quantity (17). When making quantitative judgments, primates' perceptual systems may favor discrete object-based numerosity over surface dimensions like area and size. Primates dedicate more cortex to objects than surfaces (18), and because number is a quantitative dimension that operates over discrete objects, it could complement the naturally object-based parse of the primate world.

Object-based perceptual constraints might originate from visual biases, but an *object* is a cognitive construct recognized across modalities (19). Objects can be distinguished spatially and temporally, and are identified and localized by their physical signals from many modalities. Thus, the discrete object bias in processing quantity is not necessarily limited to one modality and could affect quantity representations across modalities. Fundamental object-based constraints on cognitive processing might make numerical quantities more salient to primates than other continuous and surface-based quantitative dimensions (17).

Consistent with this claim, in a recent study, nonhuman primates, human children, adults from the United States, and adults from an Amazon culture in which counting is not routine (Tsimane) all were biased to use numerical value over surface area in a categorization task (17). Participants in each group received the same task (Figure 1A). During training, they were shown arrays in which the number of items and the cumulative surface area of the items were correlated. Participants viewed an array of dots and were given feedback to categorize small number with small cumulative area arrays as Category A and large number with large cumulative surface area arrays as Category B. After they were proficient with this training task, they were occasionally presented with stimuli in which number and cumulative surface area were uncorrelated (e.g., a large number with a small cumulative surface area) and were asked to categorize the stimuli. Monkeys, 4-year-olds, Tsimane adults, and U.S. adults were all more likely to choose categories based on the numerical value of the stimulus rather than its cumulative surface area (Figure 1A). In follow-up analyses, the number of items influenced behavior more than the element size, spatial extent, and density of the arrays. These results suggest that basic constraints on primates' perception influence number representation in humans, despite differences in their experiences with *number*.

Similarly, in another study, human infants extracted numerical quantities more easily from a set of objects than surface quantities. In their first year, human infants are sensitive to a variety of quantitative dimensions, including numerosity, surface area, brightness, loudness, and duration (6, 20), but are exceptionally sensitive to numerosity (21). Newborns can detect changes in the numerosities of sets across sensory modalities,

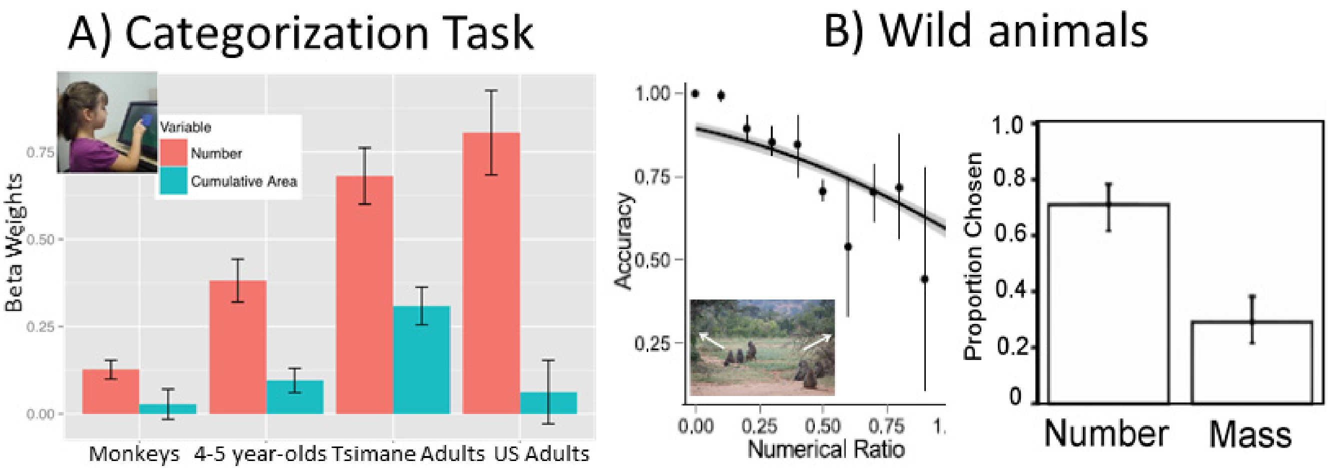

Figure 1. (A) U.S. adults, Tsimane adults, U.S. children, and monkeys were trained to categorize dot arrays based on overall quantity—they could use number, cumulative surface area, or a combination of both dimensions. Then number and cumulative area were occasionally uncorrelated in the stimuli. Each group showed a greater decision weight on the numerical dimension compared to the surface area dimension (17). (B) Wild baboons' accuracy in choosing the larger subgroup was modulated by numerical ratio. The percentage of trials on which wild baboons chose the subgroup with the larger number or mass during cases in which those dimensions were deconfounded shows a number bias (15). [Color figure can be viewed at wileyonlinelibrary.com]

from visual sets to auditory sequences (13). And although infants can detect quantitative changes in both number and surface area, they require a proportionally greater change in surface area compared to number to detect those changes (21). If number and area were equally weighted in infants' perception, number and surface area would be equally easy to discriminate on a ratio scale. The finding that monkeys, human infants, and people from non-numerate cultures are spontaneously more sensitive to number than to surface area suggests that evolutionary constraints on primates' perception are responsible for the robust perception of number.

Evidence from the decisions of wild primates reinforces this argument and also offers clues to the adaptive value of *number* as a system of conceptual representation. In a recent study of wild baboons, numerical reasoning emerged spontaneously in primitive environments (15). Baboons that wore collars with global positioning systems were monitored as they traveled in small subgroups and with the larger troop. The baboons decided about the direction of travel democratically, following the subgroup with the most individuals. The baboons' behavior in choosing which subgroup to follow showed the ubiquitous signature of Weber's law: Accuracy at choosing the larger quantity decreased as the numerical values of the subgroups became more similar (15). Figure 1B shows that the baboons' accuracy selecting the numerically larger subgroup decreased with the numerical ratio between subgroups (i.e., lower accuracy choosing the larger group as the numerical ratio approached 1.0).

The baboons' decisions were based on number rather than total mass. For a group of animals, the number of individuals is highly correlated with their total body mass (R = .96). Animals could learn this correlation between number and mass from the environment, but despite the high natural correlation between dimensions, baboons chose primarily based on numerical value (not mass) in cases where mass was equated between sets or greater for the numerically smaller set (Figure 1B). These data show that wild animals are biased to use *number* over alternative dimensions like mass to make everyday decisions, meaning that animals can disentangle highly correlated dimensions when solving a natural problem.

The fact that monkeys, infants, children, and adults from different cultures are sensitive to numerical values during set discrimination—independently of other dimensions—suggests that *number* is a key dimension in primates' perception. This does not mean that other dimensions are not represented in primates' set perception, just that they may not be as useful (compatible with other systems, efficient, flexible, reliable, abstract) for representing quantity.

NEURAL CONSTRAINTS INFLUENCE QUANTITY REPRESENTATION

If the human ability to approximate number is primitive and dates back to a common ancestor with other primates, then we would expect it to rely on common neural systems across primates. Indeed, neural similarities between humans and nonhuman primates suggest that numerical cognition has a common origin rather than arising from convergent evolution in primates. This is important because neural organization constrains how numerical information passes through and is processed by the nervous system.

In humans and nonhuman primates, common neural areas within the intraparietal sulcus and the prefrontal cortex are engaged during numerical discrimination. In monkeys, intraparietal areas (ventral and lateral intraparietal, VIP and LIP) contain neurons sensitive to numerosity. Responses of neurons in the LIP are modulated by the absolute numerical value of a stimulus (22). Responses of neurons in VIP are coarsely tuned to preferred cardinal values and modulated by the relative numerical value of a stimulus to the preferred numerical value (23). As shown in Figure 2A, the firing rate of neurons in monkeys' VIP regions peaks at a preferred numerical value (1.0 ratio), and the firing rate to other numerical values diverges from the peak as a function of the ratio between the value presented and the neuron's preferred value. Human adults show neural tuning to numerosity in functionally overlapping regions of the parietal cortex (24). Neural responses in humans (as seen with functional magnetic resonance imaging [fMRI]) are modulated by the relative values of numerical stimuli and, like neural responses in monkeys, follow a ratio-dependent neural tuning curve.

A second prediction of evolutionarily primitive mechanisms is that they should emerge early in development (25). In a recent study, 3- to 6-year-old children were tested in an fMRI adaptation paradigm in which they saw a constant sequence of dot arrays that typically had the same numerical value, shape, surface area, and dot color (26); the number, surface area, or dot color of the elements would change occasionally. The intraparietal sulcus responded more strongly to numerical changes than to other types of stimulus changes, even in 3- to 4-year-olds. The children's neural responses to numerical changes formed a curve (Figure 2B), and were predicted by the same model of neural tuning that explains neural responses in monkeys. Regions of the intraparietal sulcus that showed neural tuning in children did not show neural tuning to surface area or brightness; tuning to those dimensions was observed in separate brain regions. Thus, the neural mechanism of numerosity representation emerges early in development, signifying that it is a primitive mechanism. This is not to say that the mechanisms do not change over development—in several studies, lateralization and sensitivity to numerosity are refined with experience (27). However, establishing the neural mechanisms for numerical representation is well under way by 3–4 years, before children have any regular formal use of number. Related work with human infants suggests that number-sensitive neural regions could develop even earlier (28–30). These early-developing neural substrates of quantitative cognition play a role in counting and mathematics in adults (31).

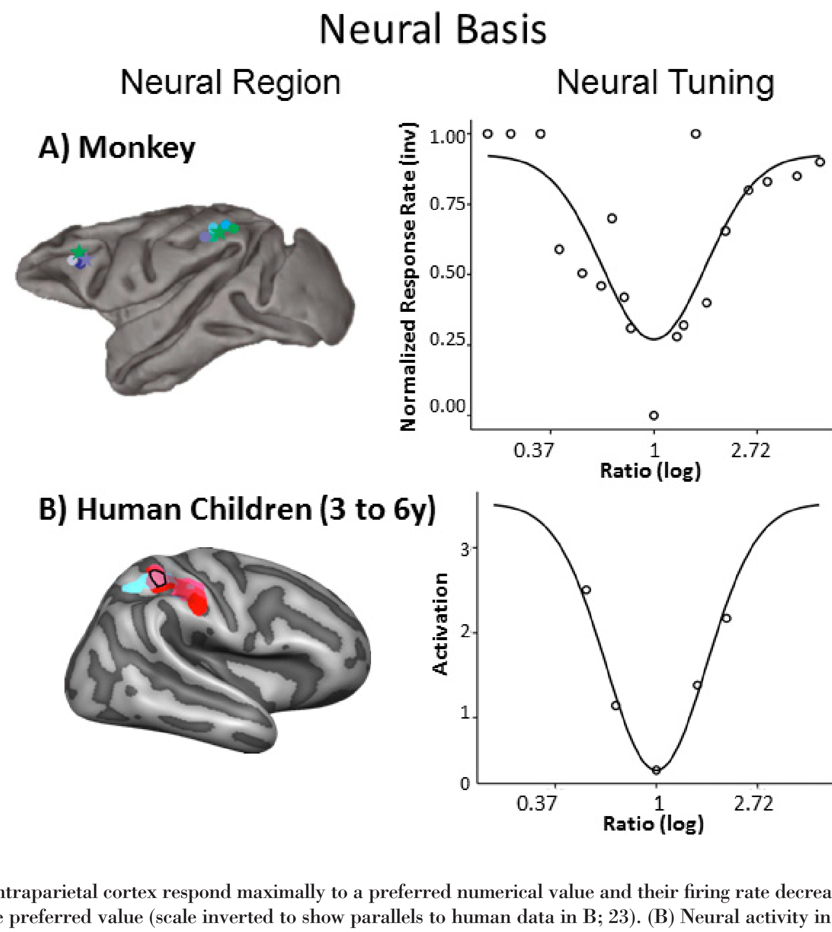

Figure 2. (A) Neurons in intraparietal cortex respond maximally to a preferred numerical value and their firing rate decreases as a function of the numerical ratio of a stimulus to the preferred value (scale inverted to show parallels to human data in B; 23). (B) Neural activity in intraparietal cortex in 3- to 6-year-olds is modulated by the numerical ratio between a standard stimulus and a novel stimulus (26). [Color figure can be viewed at wileyonlinelibrary.com]

Another sign that the course of numerical development in humans has a primitive basis is that the ability also develops during infancy in monkeys and its trajectory follows the standard 3:1 ratio of human to monkey development (32). In the domain of physical growth and motor behavior, monkeys mature much faster than humans. For example, infant monkeys reach for occluded objects by 4 months, two to three times faster than human infants, who reach at 9–12 months. Numerical cognition develops at a similar interspecies ratio. The ability to make quantitative choices emerges within the first year in monkeys, and 1-year-old monkeys' quantitative sensitivity is similar to that of 2- to 3-year-old human children. Together with data from human infants showing early numerical representation, these data from infant monkeys suggest a shared evolutionary basis for the rapid development of quantity representation in primates.

HUMAN COUNTING INTERFACES WITH PRIMITIVE QUANTITATIVE COGNITION

Human children ultimately achieve a level of facility with numerical values that has not been achieved by any nonhuman animal, even after years of symbol training (33–35). Symbolic representations of numbers emerge in humans that afford logical inferences about the discrete and ordinal properties of numerical sequences. That kind of symbolic logic is not easily acquired by other species.

Such species differences in numerical representation are consequences of humans' symbolic experience, specifically the rich cultural numeracy of the human species (36). As described earlier, nonhuman primates, human children, Tsimane adults, and U.S. adults are biased to segregate number from other dimensions as a basis for categorizing during a nonverbal task (Figure 1A). However, the nonverbal perception of number is significantly stronger in humans than in nonhuman primates. The degree of perceptual bias for number in humans is related to their mathematics experience. In Tsimane adults and U.S. children, math education predicted the degree of nonverbal number bias (Figure 3). The direction of causation for the number bias was likely from symbolic number experience to numerosity representation because in the Tsimane adults, exposure to formal math was measured by the amount of schooling an individual received, which is circumstantial, not based on merit. Thus, symbolic math concepts likely enhanced numerosity representation in the Tsimane, not the other way around.

In other studies, humans' primitive nonverbal number capacities influenced their formal, symbolic math abilities (37–39). For example, adults trained on approximate arithmetic with numerosity stimuli subsequently improved in symbolic arithmetic performance (38), showing that experience with nonverbal numerosities improves symbolic numerical abilities. Acuity in judgments about numerosity also is correlated with math performance in children (Figure 3). Together, these data suggest that interactions between number representations are likely bidirectional: Nonverbal numerical cognition influences verbal mathematics concepts and experience with mathematics concepts enhances nonverbal numerical capacities (40).

Evidence that nonverbal numerosity estimation is related cognitively to symbolic numerical processing suggests that primitive numerical systems interact with symbolic math processes during the modern human life span. Several different types of contact between those representational systems could yield the observed cognitive interactions, including direct semantic mapping between representations (41–43), shared principles of counting and estimating (4), ordinality (44, 45), and basic logical algorithms (46). The nature of the relation between nonverbal numerosity representations and symbolic numerical

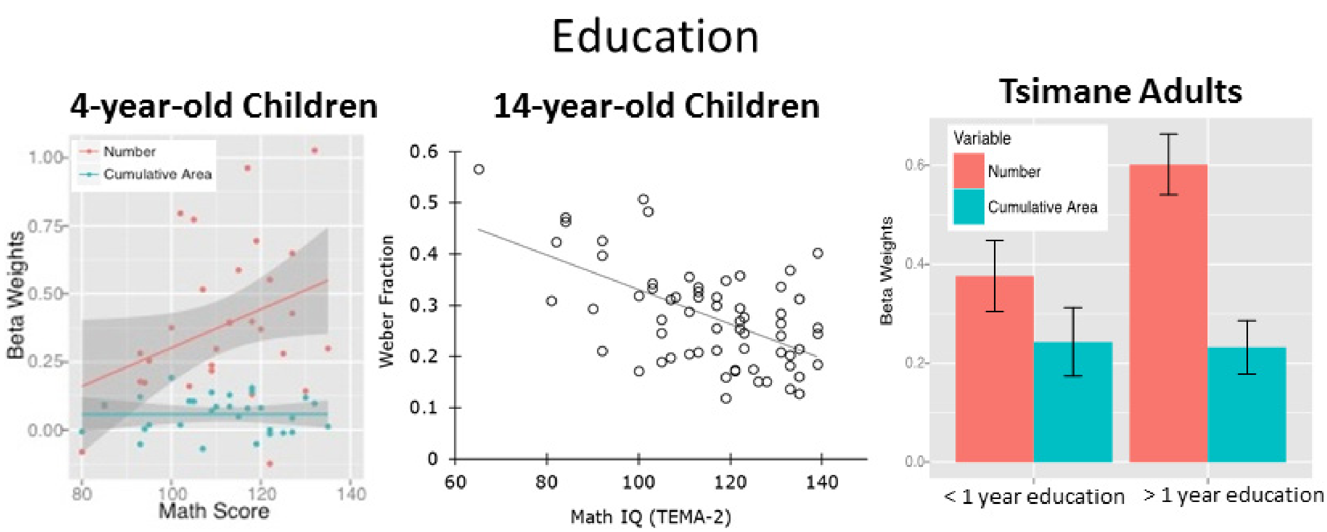

Figure 3. Mathematics education enhances numerical perception in 4-year-olds (left; 17), older children (middle; 37), and Tsimane adults (right; 17). [Color figure can be viewed at wileyonlinelibrary.com]

representations is central to understanding the influence of evolutionary constraints on modern human mathematical thought.

CONCLUSION

Children initially approach the problem of counting with their primate brain, and whatever processing biases it has, along with acquired knowledge and the flexibility to learn. Children share with other primates perceptual biases to quantify sets of discrete objects numerically and basic logical mechanisms for operating on quantitative information. These basic perceptual and logical faculties come from a brain that evolved a sophisticated object-based visual system to solve natural problems simply and reliably, some of which are quantitative—these are conditions ripe for number representation. These basic constraints continue to influence how modern humans think about quantities throughout their lives, even in the symbolic mode. Evolutionary constraints on human cognition shape the acquisition of counting in human children and likely made counting possible over the course of human cultural evolution.

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