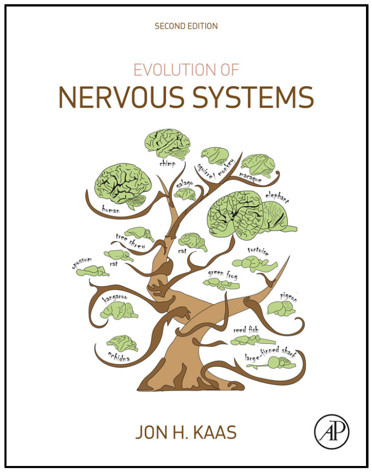

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3.27 Evolutionary Constraints on the Emergence of Human Mathematical Concepts

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Abstract

Nonhuman animals and humans share many kinds of insights about the physical world. One of those is the ability to reason logically about the number of items in a set of physical objects. Current research suggests that nonverbal numerical reasoning about physical objects is the first type of numerical cognition that emerges in human development and it influences the development of children's formal numerical concepts such as verbal counting and arithmetic. Comparative research between humans and nonhuman primates can help us gain an understanding of the evolutionary origins of primitive mathematical concepts in humans, and characterize the basic algorithms that support the emergence of mathematical reasoning over human development. In this chapter we describe current knowledge from comparative cognition and neuroscience about the genetic/maturational, environmental, and evolutionary factors that underlie early mathematical concept development in humans.

3.27.1 Primitive Concepts of Number

Humans differ from other species in their use of symbolic systems. This difference is apparent in the domain of mathematics where humans have unique and elaborate formal symbol systems for counting, arithmetic, logic, and spatiotemporal reasoning (and beyond). Immersion in the formal mathematical system begins early in development for most human children. Children are introduced to verbal counting beginning at around 2 years of age and by 4 or 5 years of age they are introduced to arithmetic (Mathematics Learning Study Committee, 2001). Substantial research has shown that children are not limited to learning numerical concepts through these formal systems but simultaneously possess intuitions about numerical value through nonverbal, nonsymbolic mechanisms.

Before children can verbally count they can discriminate sets of objects nonverbally by comparing the relative number of objects in each set (Xu and Spelke, 2000; Cordes and Brannon, 2008; Izard et al., 2009). For example, infants rely on the number of previously presented items when deciding how long they should search for those items hidden inside a box (Feigenson and Carey, 2003). Infants watched as items were being placed in a box and were then allowed to reach in and pull out the items. On some trials, researchers secretly removed one or more of the items. The infants searched the box longer when there was a missing item as long as the total number of items placed in the box was three or less. Infants can also estimate the outcomes of simple arithmetic transformations over sets of objects. For example, they understand that two objects added to a set of two objects matches a set of four objects, not a set of two or eight objects (Wynn, 1992; McCrink and Wynn, 2004). These same numerical abilities are present in nonhuman animal behavior. Animal research has shown significant parallels between the nonverbal numerical reasoning abilities of humans and nonhuman animals (Dehaene, 2011; Brannon, 2006). For example, monkeys were trained to touch stimuli consisting of one to four items in ascending order (Brannon and Terrace, 1998). They were then able to transfer this ability to novel and larger sets of five to nine items. Many nonhuman animals, which lack language and counting systems, can compare sets of objects numerically (birds: Pepperberg, 1987; Scarf et al., 2011; fish: Piffer et al., 2012; monkeys: Jordan et al., 2005; Cantlon and Brannon, 2006; Beran, 2007; Barnard et al., 2013; chimpanzees: Matsuzawa, 1985; Boysen and Berntson, 1989; Beran, 2001).

This nonverbal, nonsymbolic representation of number is only an approximation of numerical value unlike the precise numerical representations that arise from symbolic counting. When a person verbally counts a set of objects they can determine the exact number of objects in the set and can make distinctions between sets that differ by one item no matter how large those sets are. This is not the case for *nonverbal* numerical discrimination. Analyses of the error patterns of human children and nonhuman animals show that their nonverbal numerical representations are noisy and imprecise—akin to analog machine representations of intensity values (Beran, 2007; Cantlon and Brannon, 2006; Gallistel, 1990; Gelman and Gallistel, 2004; Emmerton et al., 1997; Meck and Church, 1984; Nieder and Miller, 2003; Tomonaga, 2008). When animals or humans make numerical judgments in the absence of verbal counting, their accuracy is limited by the ratio between the numerical values being compared. For example, one might be 80%

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accurate at choosing the numerically larger of two sets when the numerical choices are 5 versus 10, 10 versus 20, or 50 versus 100 (a 1.0 ratio change) but might perform at 50% when the choices are 4 versus 5, 16 versus 20, and 40 versus 50 (a 0.25 ratio change). This ratio-dependent pattern of success and failure is known as Weber's law. The proportion numerical difference a subject needs to successfully discriminate sets is known as their Weber fraction. Research has shown that the average Weber fraction for 6-month-old infants is about 1.0 (2:1 ratio), for 3-year olds it is 0.5 (2:3 ratio), and by adulthood it is 0.11 (9:10 ratio; Brannon, 2005; Halberda and Feigenson, 2008).

Sensitivity to numerical quantity in human infants and nonhuman animals is taken as evidence of an evolutionary basis for numerical processing in humans. Human infants and nonhuman animals lack experience with human culture and thus their numerical sensitivity cannot be derived from language or cultural learning. The common behavioral signature of Weber's law in numerosity discrimination suggests that human infants and nonhuman animals have a common solution and shared cognitive mechanisms for numerosity perception. The fact that the numerosity mechanism is shared across primate species and develops early in humans suggests that it is part of our evolutionary endowment.

3.27.2 Genetic Maturation

One question in human cognitive development is whether nonverbal numerical reasoning in humans is really innate. Although infants can demonstrate sensitivity to quantity early in development in looking time paradigms, it is not until years later that they are capable of tasks requiring them to make explicit choices about quantity, such as choosing the larger quantity from a set of options.

Researchers have shown that infants are sensitive to changes in number using implicit measures such as looking time within the first year of life and as early as 2 days postnatal (Brannon, 2002; Izard et al., 2009; Xu and Spelke, 2000; Cordes and Brannon, 2008). For example, researchers first habituated 6-month-old infants to a visual array of dots (Xu and Spelke, 2000). Once habituated, infants were shown two different dot arrays: one that differed in the number of dots and one that had the same number of dots. Infants preferentially looked toward the stimuli with a new numerosity if the number of items differed by at least a 1:2 ratio. Infants are sensitive to differences in number over sets of objects when the stimuli vary in size or shape, and even when they are presented across modalities (Brannon et al., 2004; Cordes and Brannon, 2009; Izard et al., 2009).

Although infants are sensitive to numerical differences using implicit measures such as looking time, they are unable to make accurate explicit choices until about the age of 2.5–3 years (Izard et al., 2009; Brannon and Van de Walle, 2001; Feigenson and Carey, 2003; Feigenson et al., 2002; Mix et al., 2002; Sella et al., 2015). For example, 1-year-old children presented with two sets of crackers spontaneously chose the larger set if both sets were between one and three items (Feigenson and Carey, 2003). When one of the sets was larger than three items (eg, 2 vs. 4 or 3 vs. 6), the 1-year olds were unable to discriminate between the sets. From about 14 months until 2.5 years old, there is a gap in the literature due to difficulties with testing children in this age range. Not until 2.5–3 years of age are children able to make accurate numerical judgments about more versus less across both small and large sets of quantities (Cantlon et al., 2010; Halberda and Feigenson, 2008; Sella et al., 2015). The length of time it takes children to develop the capacity to judge numerosity by making task-based choices raises questions about whether there is an innate sense of number in humans or if instead children require substantial learning before they can make logical choices based on numerosity (Mix et al., 2002).

Why does it take 2–3 years for human children to make explicit choices about number when they are capable of discriminating numerosities in their looking time, and of reaching, grasping, and perceiving objects much earlier? One possibility is that human children do not yet have the experience with numerosities needed to make accurate choices. Another is that there is a genetic or maturational component underlying numerical cognition, which delays development in humans.

Comparisons between infant monkeys and infant humans can help to parse the genetic and maturational, versus experiential influences on human numerical development (Bjorklund and Pellegrini, 2002; Diamond, 1990, 1991; Gómez, 2005; Rosati et al., 2014). During infancy, monkeys mature much faster than humans due to differences in genetic maturation. It takes 8–10 months for human infants to crawl, but monkeys can crawl within the first month of life (Hinde and Spencer-Booth, 1967). Similarly, monkeys are able to locate occluded objects three times earlier in infancy than human infants (Diamond, 1990, 1991; Gómez, 2005). In an A not B task, subjects watch as one of two wells is baited with a food item (Diamond, 1990). After a delay, they are allowed to reach for one of the two wells. Human infants do not pass this test until the age of 9 months if no occluder is used during the delay period and until 12 months if an occluder is used. In contrast, infant monkeys successfully complete the task without an occluder by the age of 2 months, and with the occluder by 4 months. These tasks rely on an interaction between the prefrontal cortex and the medial temporal lobe (Weinstein et al., 1988). Total brain volume and white matter growth occur three times faster in infant monkeys than infant humans (Malkova et al., 2006), so the differences seen between the infant humans and monkeys on these tasks are likely due to relative immaturity of the human infant brain (Malkova et al., 2000; Diamond, 1990). In contrast, social development is slower in infant nonhuman primates than in infant humans. Infant humans follow others' gazes by 6 months of age, a skill that takes twice as long to develop in chimpanzees (Butterworth and Jarrett, 1991; Okamoto et al., 2002). Thus, in cases such as perceptual and motor development where fundamental genetic maturation is known to have a strong influence over development, monkeys develop abilities faster than humans. But in cases where specific experiences are thought to be critically important, like the development of social cognition, humans can show a developmental advantage over monkeys.

We capitalized on these developmental differences between humans and monkeys to examine whether number perception is dependent on the neural maturation rate of a species. If number perception, like object perception, relies on the maturational rate, then it should develop faster in monkeys than in humans (about three times earlier). Moreover, if number perception is a fundamental developmental skill with an innate basis, then it should develop as early as possible within the known maturational constraints of the species.

To test this, infant and adult baboons were given a food choice task in which they were presented with two sets of food items ranging from one to eight items (Ferrigno et al., 2015). The monkeys chose one set by touching a port directly in front of the set (Fig. 1A). They received the items in the chosen set regardless of whether they chose the more numerous of the two sets or not. Thus, they did not receive differential reinforcement or numerical training. Infant monkeys accurately and spontaneously chose the larger of two sets of food items and showed ratio-dependent accuracy—they were more likely to choose the larger set when the ratio difference between the sets was large. Interestingly, we found no differences between the performance of adult and infant monkeys on this task. The fits for infant and adult monkey accuracy as predicted by Weber's law are shown in Fig. 1B. Both groups showed an effect of numerical ratio on performance, yet there were no differences between groups. Infant and adult monkeys also had the same overall accuracy and sensitivity to ratio differences between the sets (Fig. 1C and D). Thus, monkeys' spontaneous number skills are largely developed by 1 year of age and remain relatively stable in the adulthood.

We then compared the performance of the infant monkeys with prior data from human infants. The development of numerical abilities in monkeys was much faster than humans. Infant monkeys made accurate numerical judgments on sets of items that human infants fail to discriminate until 2.5–3 years of age. Before 2–3 years, children do not discriminate between sets of items when comparing large quantities (more than three items) in explicit choice tasks (Feigenson and Carey, 2003; Sella et al., 2015). Infant monkeys were capable of explicit numerical choices with large numbers up to eight items after just 1 year of experience. If infant monkeys can gain the experience necessary to make numerical judgments with just 1 year of experience with the physical world, then a human infant should also be able to gain the experience necessary within 1 year. By 1 year, human infants have had as much or more experience with the physical world (and quantities) than infant monkeys. Humans' slow-developing numerical system is likely not due to lack of experience. Instead, we see that the difference in the pace of numerical development between monkeys and humans is similar to that of their perceptual, motor, and neuroanatomical development. One-year-old infant monkeys' numerical abilities were equivalent to those of a 2.5- or 3-year-old human child. This threefold difference in developmental rates between species suggests that like perceptual development, the development of numerical abilities is limited by the genetic maturation rate of the species.

Animals and humans are capable of representing numerosity very early in life. However, the developmental timeline of these skills differ between species. Monkeys, who mature faster than humans, develop numerical abilities earlier in life. This developmental difference is likely due to the cognitive and neural maturation differences between species. The link between neural maturation and numerical perception suggests that number perception develops as early as possible for a species.

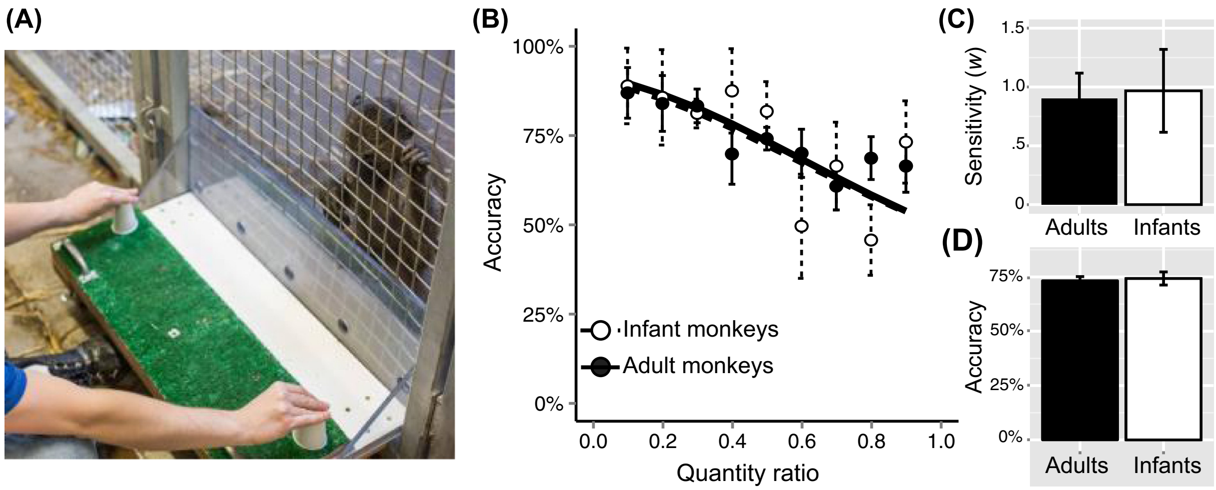

Figure 1 (A) An infant monkey is tested on the numerical choice task. (B) Infant and adult accuracy as a function of the quantity ratio (smaller quantity/larger quantity). *Solid lines* (adults) and *dotted lines* (infants) represent the fits predicted by a model of Weber's law. (C) The average Weber fractions for infant and adult animals. Smaller w values signify better performance and a more sensitive approximate number system. (D) Overall accuracy for infant and adult animals. Error bars represent the standard error of the mean. Figures B–D were reprinted from Ferrigno, S., Hughes, K.D., Cantlon, J.F., 2015. Precocious quantitative cognition in monkeys. Psychon. Bull. Rev. 1–7, with permission of Springer.

3.27.3 Experience

The slow time course of human infants' and toddlers' nonverbal numerical development appears to be affected by genetic maturation, as indicated by the comparatively rapid pace of numerical development in infant monkeys versus infant humans described in the previous section. After children initially develop the ability to make explicit judgments of numerosity, there is further developmental change in the precision with which they discriminate numerical stimuli. Human children show a gradual increase in numerical sensitivity into adolescence (Halberda and Feigenson, 2008). As mentioned, 2- to 3-year-old children discriminate numerical values at a 2:3 ratio (0.6 Weber fraction). At 18 years of age, humans discriminate values at a 9:10 ratio (0.11 Weber fraction). This is well beyond the precision of discrimination shown even in highly trained monkeys, suggesting that there is something unique about human numerical development compared with that of monkeys that allows human numerical perception to become far more precise than that of nonhumans.

Studies that measure the effects of training on numerical discrimination in humans and nonhuman primates have shown that experience is a critical factor in the precision of individuals' numerical representations. Training studies with nonhuman animals have shown that practice with numerical discrimination rapidly improves animals' numerical representations (Tomonaga, 2008; Barnard et al., 2013; Cantlon et al., 2015; Ferrigno et al., 2015). Recently, we trained two monkeys for over 120 days and 20 000 trials on a numerical match-to-sample task. As testing progressed, both monkeys became increasingly accurate (Fig. 2A). Performance improvements were not limited to overall accuracy but also were observed in psychophysical discrimination sensitivity. At the beginning of training, animals were only able to discriminate differences of a 2:5 ratio. After receiving experience with a number matching task, the animals were able to discriminate between sets at a 3:4 ratio—their sensitivity nearly doubled as a result of training. Within subjects, Weber fractions became smaller (more precise) as training progressed (Fig. 2B). This means that the animals did not simply improve their ability to execute the task rule, but their representations of specific numerical values sharpened.

Multiple studies provide convergent evidence that with training, monkeys come to discriminate numerical differences of about a 3:4 ratio (Nieder and Miller, 2003; Cantlon and Brannon, 2006). This is a greater sensitivity than the average 4-year-old human child (Halberda and Feigenson, 2008). On average, it takes human children 4.5–5 years to develop numerical sensitivity as fine as a 3:4 ratio (Fig. 3; Nieder and Miller, 2003; Cantlon and Brannon, 2006; Halberda and Feigenson, 2008). Additionally, studies with extensively trained chimpanzees found even more precise Weber fractions in nonhuman primates, at the discrimination level of a 6:7 ratio (Weber fraction = 0.17), which is comparable with that of 6-year-old human children (Tomonaga, 2008). Although it is difficult to compare chimpanzees with monkeys using existing data because the duration of training and tasks differed between studies, the data could suggest that apes are capable of achieving a higher level of discrimination sensitivity than monkeys. The reason to suspect differences in numerical abilities between species is that even with substantial training no nonhuman primate has reached a level of numerical discrimination sensitivity equal to adult humans, suggesting species-specific limitations on numerical learning.

Number training effects on the precision of numerosity representations are also observed in human adults and children. Adults who were trained on a numerosity comparison task in which the numerical values gradually became closer together on a ratio scale improved their sensitivity to numerical value twofold (DeWind and Brannon, 2012). Similarly, children with dyscalculia who played numerosity discrimination games for a total of 8 h subsequently showed increased discrimination acuity during nonverbal numerical judgments (Wilson et al., 2006). Thus, both human and nonhuman primates show experience-dependent changes in nonverbal number representation. With or without training, however, human adults reach

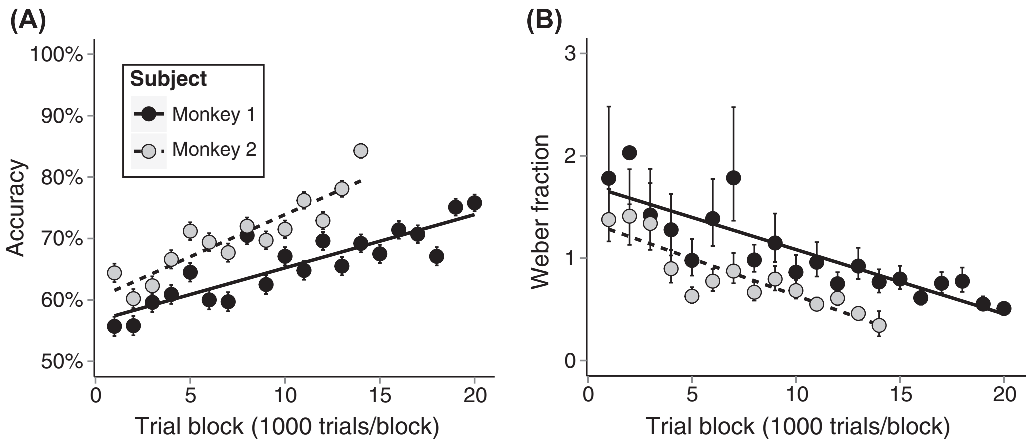

Figure 2 Training effects were seen in both (A) overall accuracy for each monkey tested and (B) Weber fractions as training progressed. Smaller *w* values signify better performance and a more sensitive approximate numerical system. *Solid* and *dotted* lines represent a linear fit. Error bars represent a bootstrapped 95% confidence interval. Unpublished data from the Cantlon Lab.

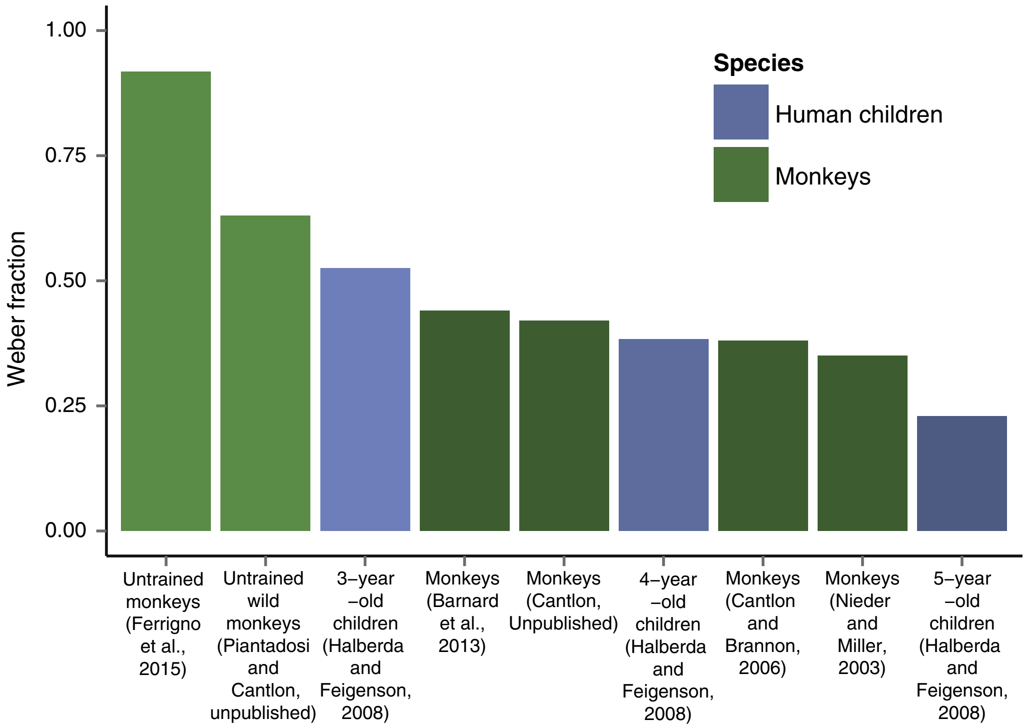

Figure 3 A comparison of Weber fractions of children and monkeys. Smaller *w* values signify better performance and greater numerical sensitivity. Untrained monkeys performed similarly to 3-year-old children, whereas trained monkeys perform as well as 4-year-old human children. (Weber fractions of the children were from Halberda, J., Feigenson, L., 2008. Developmental change in the acuity of the "number sense": the approximate number system in 3-, 4-, 5-, and 6-year-olds and adults. Dev. Psychol. 44, 1457–1465.). Monkey Weber fractions were from three separate groups of trained rhesus macaques (Cantlon and Brannon, 2006; Cantlon, unpublished; Nieder and Miller, 2003), baboons with extended exposure (Barnard et al., 2013), untrained baboons (Ferrigno et al., 2015), and untrained wild baboons (Piantadosi and Cantlon, unpublished).

a level of nonverbal numerical sensitivity that surpasses any shown by a nonhuman animal. One explanation, based on these findings from training studies, is that humans get more experience making nonverbal numerical discriminations than other primates. A second major difference between humans and other species, however, is that most humans are immersed in a culture of counting and symbolic numerical computation. The ability to represent number exactly, as is done with counting, could facilitate nonverbal numerical discrimination in humans.

As children develop the capacity for symbolic number representation, the precision of their numerosity representations improves beyond the level of nonhuman primates. Studies have investigated how these primitive nonverbal numerosity abilities and formal mathematics skills relate (Halberda et al., 2008; Marle et al., 2014; Park and Brannon, 2014). One study looked at whether approximate number abilities predict early formal mathematics learning in preschool children (Marle et al., 2014). They found that children's approximate number acuity (Weber fractions) predicted formal math achievement 1 year later. Similarly, training on approximate number system tasks affects symbolic math performance (Park and Brannon, 2014). Adults who received training on approximate addition and subtraction number task for 10 sessions had improved symbolic addition and subtraction skills compared to those who did not. These studies suggest a psychological connection between primitive numerosity abilities and symbolic counting. Transfer of learning between nonsymbolic and symbolic numerical representations in humans could be a cause of humans' more precise nonverbal numerical abilities compared with monkeys.

3.27.4 Innate Constraints

Number is unique compared to other intensity dimensions such as surface area or rate because it is an abstract quantitative representation that cuts across sensory modalities, space, and time. There are many types of quantitative representations that could be used to compare sets of objects. For example, cumulative surface area, density, duration, and rate are all often correlated with numerical value in nature. Sets that have a greater number of objects are often denser, have a higher rate or greater duration, and take up more space or surface area. However, many of these nonnumerical dimensions are limited to representation by only a subset of sensory modalities. For example, 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, and over space or time. Unlike rate (temporal) or density (spatial), a numerical sum can be calculated from sets distributed over space and time. The flexibility that the numerical dimension affords in terms of cognitive processing could make it an optimal dimension for comparing sets of objects under naturalistic conditions such as occlusion, interruption, and integration of sets across the senses, space, and time.

Nonhuman animals have been shown to represent numerical values across sensory modalities and across sets distributed in space and time. For example, monkeys were trained on a matching task with flashing dots sequentially presented on a screen or as auditory tones (Jordan et al., 2008). Monkeys matched the number of sequentially presented visual or auditory "items" to a spatial array of visual items with the same numerical value. Interestingly, the monkeys were just as accurate in the auditory–visual condition as they were in the visual–visual condition—there was no cost in accuracy for the monkeys to respond in a different modality. Additionally, animals made accurate numerical judgments even when presented with mixed audiovisual sequences of flashing dots and beep sounds. These data show that nonverbal number representations are abstract across sensory modalities and space and time for nonhuman primates. Similar results have been obtained from human children (Barth et al., 2005; Jordan and Brannon, 2006).

Historically, researchers have asked whether, given all the possible nonverbal dimensions available to quantitatively compare sets, animals use "number" at all (Davis and Memmott, 1982; Davis and Pérusse, 1988; Breukelaar and Dalrymple-Alford, 1998; Seron and Pesenti, 2001). To answer this, many researchers have tested whether animals could make quantity judgments when alternative visual quantitative dimensions were controlled. In some studies, researchers compared animals' performance on numerosity discrimination tasks in which cumulative surface area, density, duration, and individual element sizes were correlated versus uncorrelated with the numerosity values (Emmerton et al., 1997; Brannon and Terrace, 1998; Judge et al., 2005; Cantlon and Brannon, 2006; Jordan et al., 2008; Scarf et al., 2011). They found that nonhuman animals could discriminate numerosity regardless of whether those alternative dimensions were correlated or uncorrelated with numerosity. Due to the complex correlations among multiple quantitative dimensions, it often is not possible to control for all nonnumeric quantitative dimensions within a single trial. Instead, researchers take one dimension, for example, cumulative area and make it incongruent (eg, larger area with the smaller number) on 50% of trials, and congruent (eg, larger area with the larger number) on the remaining trials. Some have argued that animals could combine multiple nonnumerical cues or switch cues from trial to trial to identify the larger numerosity without ever representing numerosity directly (Gebuis and Reynvoet, 2011, 2012). This argument is problematic because subjects would have to know the direction of the relations between numerosity and the alternative cues (eg, larger numerosity with greater density and smaller element size) and the congruency between numerosity and the alternative dimensions. This explanation is unlikely because animals are naturally and spontaneously sensitive to changes in number even when no differential reinforcement is given for discriminating number (Cantlon and Brannon, 2007; Tomonaga, 2008; Cantlon et al., 2015; Ferrigno et al., 2015).

There is evidence that, given alternatives, number is the preferred quantitative dimension used by primates during decision making (Cantlon and Brannon, 2007; Burr and Ross, 2008; Anobile et al., 2015; Ferrigno et al., 2015). These data show that animals use numerical information to discriminate between stimuli even when other cues are available. In one study, monkeys were trained on a matching task in which they saw a picture and then had to choose a matching picture from two choices (Cantlon and Brannon, 2007). After training on the matching task (**Fig. 4**: Standard Trials), researchers tested the animals on trials in which there was more than one correct choice (**Fig. 4**: Probe Trials). One choice matched on number, while the other matched on an alternative dimension, such as color, shape, or surface area. Animals were reinforced for either choice, and thus were not experimentally biased to choose one match over the other. Monkeys more often chose the number match, as long as there was a large enough ratio difference between the two numerosities presented. When number was easy to perceive (large difference ratio between the match and distractor), the monkeys used number even though other cues were available. When number was hard to perceive (small difference ratio), monkeys were more likely to match based on alternative dimensions. These results suggest that animals perceive multiple stimulus dimensions, including the numerical dimension, and they use numerical information spontaneously even when other cues are available. These findings also provide a possible explanation for previous results that led researchers to conclude that animals do not use numerical information—animals favor use of alternative dimensions when numerical discrimination is overly difficult.

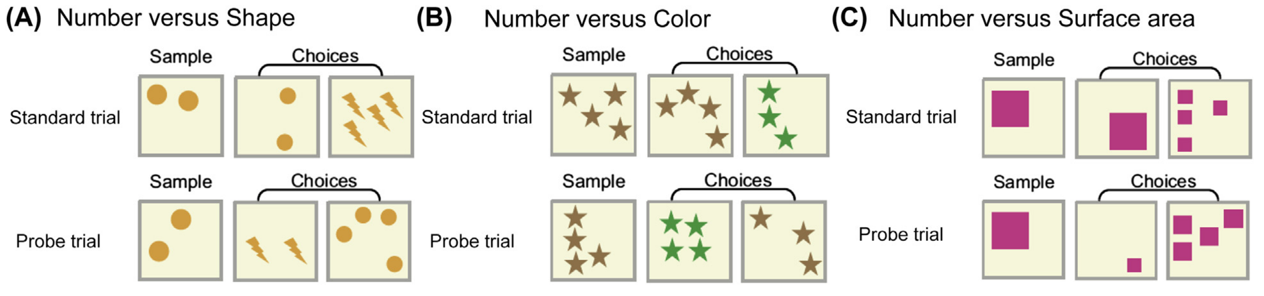

Figure 4 Sample trials for each dimensions tested against number: (A) shape, (B) color, and (C) surface area. Probe trials were nondifferentially reinforced such that either answer was treated as correct. Monkeys spontaneously represented and used numerical information over cumulative surface area as the basis for matching. Reprinted from Cantlon, J.F., Brannon, E.M., 2007. How much does number matter to a monkey (*Macaca mulatta*)?. J. Exp. Psychol. Anim. Behav. Process. 33 (1), 32.

Although nonhuman primates use a variety of dimensions to represent sets of objects, number is a powerful representation in nonhuman primates.

Research with human children has found equivalent results (Brannon et al., 2004; Cordes and Brannon, 2009; Cantlon et al., 2010; Cantrell and Smith, 2013). In a similar design, 3- and 4-year-old children were first trained on a quantitative match-to-sample task (Cantlon et al., 2010). During training, the correct answer matched in both number and cumulative area. After training, subjects were given trials in which there were two matches: one number match and one cumulative area match. When the numerical ratio was favorable (easy to discriminate), children picked the number match more often than the area match. As the numerical ratio became harder, children were less likely to choose the number match. Human infants also show a bias to represent numerical information. Infants habituated to visual arrays with a constant number, and cumulative area of items will look longer at an array that contains a change in number compared to one that has an equal change in cumulative area (Cordes and Brannon, 2009).

Together these studies suggest that preverbal infants and nonhuman animals are sensitive to numerical differences even when other quantitative cues are present. Both nonhuman animals and preverbal infants spontaneously extract numerical information from the world, along with other forms of information like surface area. Experiences such as learning to count are not needed to bias humans or nonhuman animals to represent numerical information. Animals and preverbal infants represent number naturally without the need for explicit reinforcement or experience with numbers. Thus, the natural tendency to perceive, represent, and use numerical information is not due to human culture and has a shared evolutionary origin with nonhuman animals.

One 2016 study investigated whether numerical information is spontaneously extracted from visually presented sets when subjects are free to use multiple dimensions simultaneously as the basis for quantitative judgment (Ferrigno et al., 2015). We looked at what quantitative information subjects extracted from visual dot arrays in a categorization task. Subjects were trained to categorize dot arrays with "less" (10 dots and 10 cm^2 surface area) into one category and "more" (20 dots and 20 cm^2 surface area) into another. The number of dots and cumulative area were completely correlated during training. Thus, subjects could use number, cumulative area, or some combination of both to correctly categorize the stimuli. After training, a small number of nondifferentially reinforced probe trials were added. For these trials, the number and cumulative area of the arrays were uncorrelated. This allowed us to measure how much information from each dimension was extracted and used during categorization. Importantly, we tested a diverse sample of subjects on this task. We tested nonhuman primates, 4- to 5-year-old US children, US adults, and Tsimane' adults (from a region of the Amazon where people do not routinely count or use numerical language and thus provide an opportunity to measure cultural influences on quantity perception). We found that in all groups, the *number* of dots was used more than cumulative surface area. Follow-up experiments and analyses showed that number also was more influential on subjects' category judgments than density, convex hull, and dot size. This shows that number is a universally salient perceptual dimension for humans, beginning early in development, and independently of culture—and the saliency of number is shared by another primate species.

This bias to use numerical information in lieu of alternative dimensions likely comes from evolutionary constraints on the primate perceptual system. The primate perceptual system is object oriented—more cortex is dedicated to recognizing discrete objects rather than continuous surface properties (Peuskens et al., 2004). Number may be easy for primates to perceive because it operates over discrete objects, and their perceptual systems use discrete objects as a dominant representation. Constraints on the primate perceptual system could lead to increased saliency of numerical information over other more continuous quantitative properties.

The high perceptual saliency of numerosity could have been an important precursor to the invention of formal counting in our evolutionary history. For early humans to conceive of a counting system, they must have first perceived numerical information, isolated number from other dimensions, and had a bias to use number as a basis to quantify objects or experiences (Cantlon et al., 2015; Ferrigno et al., 2015). This perceptual bias to segregate numerical information and use it preferentially during quantification could have been an evolutionary catalyst for the emergence of a discrete numerical counting system in humans.

3.27.5 Adaptive Value

The natural functions of numerical cognition offer clues to its adaptive value as a system of conceptual representation. As described earlier, the cognitive advantages of number representation for primates are that it is a flexible representation that cuts across space and time, and it is an object-based representation that is ideally suited to the object-based nature of primate visual processing (and possibly other object-oriented birds and mammals as well). In this section, we describe some of the functions of numerical reasoning that have been observed in nature. Research on the natural functions of numerical reasoning provides insight into what could have caused numerical cognition to emerge in the first place, over human evolution. This is important because to understand the algorithms of numerical cognition we need to know what problems it was designed to solve.

Among primates, numerical perception has been suggested to be important for making foraging and social decisions. For example, wild orangutans preferentially choose to forage and spend most time on fig trees with largest number of ripe figs (Utami et al., 1997). Orangutans that forage on these fruitful trees had the highest intake rates and foraging efficiency. They ate more figs with less movement than those foraging on a less fruitful tree. Similar results have been shown using more controlled seminatural foraging experiments (Hauser et al., 2000; Hauser and Carey, 2003). When monkeys are given a choice between two different food caches, they will reliably choose the more numerous of two as long as the ratio difference is large enough. It is clear from this and other research that using numerical information provides an advantage for efficient foraging (Harper, 1982; Godin and Keenleyside, 1984; Stephens and Krebs, 1986; Symington, 1988).

Although it is more common to think of quantitative reasoning as a foraging computation, some studies suggest that numerical reasoning is important for social behavior (McComb et al., 1994; Wilson et al., 2001). Species communication is one area where researchers have observed numerical processing in the wild. Researchers have used playback experiments to see whether animals used the number of calls presented as a cue for intergroup interactions (McComb et al., 1994; Wilson et al., 2001). When animals were played a small number of calls from a hidden speaker they were likely to approach the source of playback. But if a large number of calls presented, they were less likely to approach the hidden speaker and, in some cases, tended to recruit more individuals before doing so. Another study looked at how animals make collective movement decisions by tracking the movement of individual baboons within a large troop using global positioning system (GPS) monitors (Strandburg-Peshkin et al., 2015). When baboons were faced with collective movement decisions about direction of travel, they used the number of individuals that took a specific path. A follow-up study demonstrated that the wild baboons' troop movements were truly based on *number* of individuals as opposed to mass or size, and their choice patterns showed signatures of Weber's law (Piantadosi and Cantlon, unpublished). As the ratio difference (Weber fraction) between the number of baboons in each subgroup increased, animals were more likely to choose the larger group. Thus, the animals' behavior relies on numerical information and can be accurately modeled using Weber's law.

The use of numerical reasoning in the wild is not limited to primates. In birds, numerical perception has been shown to influence nesting behaviors (Hunt et al., 2008; Odell and Eadie, 2010). In one study, researchers examined whether brood parasitic female ducks used the number of eggs to choose a target nest. Researchers set up multiple simulated nests with differing quantities/numbers of eggs in them. They found that female brood parasites chose to lay eggs in the nests with fewer eggs, which would give their offspring the best chance of survival. Fish have been shown to use numerical comparisons during schooling and collective behaviors (Agrillo and Dadda, 2007; Pritchard et al., 2001; Hoare et al., 2004). When presented with a dangerous situation, fish tend to join the larger of the two shoal options (Pritchard et al., 2001; Hoare et al., 2004). Even insects are suspected to use numerical representations in their natural behaviors (Wittlinger et al., 2006; Chittka and Geiger, 1995; Gallistel, 1990). Finally, many animals have been shown to use numerical reasoning in foraging behavior by matching their probability of visiting a food patch to the proportion of competitors versus amount of food, an optimal foraging behavior (Godin and Keenleyside, 1984; Harper, 1982). However, it is currently unclear whether true numerical reasoning is involved in many of these cases versus rate, mass, and density perception.

3.27.6 Convergent or Divergent Evolution

The many examples of quantitative and numerical reasoning in nature raise questions about whether these behaviors arise from a common origin or are instead cases of convergent evolution. Differences in the neural structures that underlie these behaviors could be informative. In humans and in nonhuman primates, common neural structures have been shown to represent numerical values during comparison tasks. Areas within the intraparietal sulcus (IPS) as well as the prefrontal cortex are engaged during numerical discrimination in both monkeys and humans (**Fig. 5**; Nieder et al., 2002; Nieder and Miller, 2003, 2004; Piazza et al., 2004; Roitman et al., 2007). In one study, monkeys were presented with visual dot arrays and trained to make same/different discriminations over numerosity (Nieder and Miller, 2004). Arrays were presented consecutively and monkeys released a response

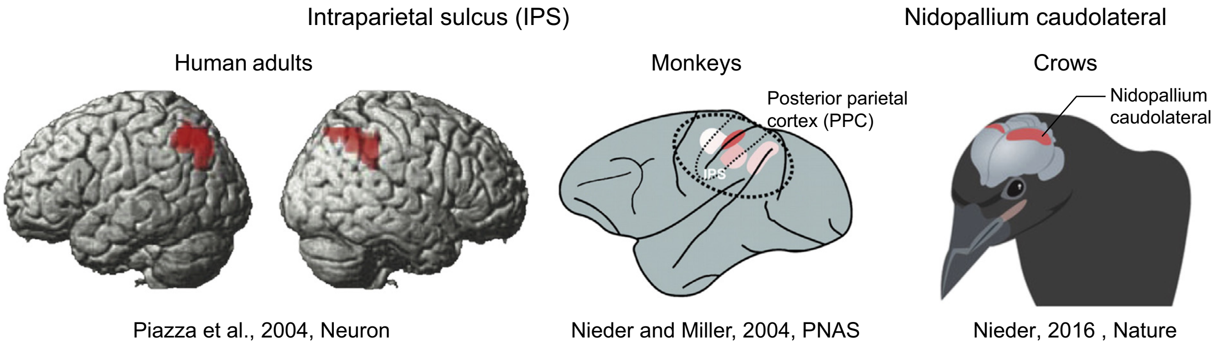

Figure 5 Neural regions that represent numerical value during approximate number tasks. Monkeys and humans show homologous areas of activation in the IPS. Crows show analogous regions of the nidopallium caudolateral. Reprinted with modifications to show parietal region activation from Nieder, A., Miller, E.K., 2004. A parieto-frontal network for visual numerical information in the monkey. Proc. Natl. Acad. Sci. U.S.A. 101 (19), 7457–7462, Copyright (2004) National Academy of Sciences, USA; Piazza, M., Izard, V., Pinel, P., Le Bihan, D., Dehaene, S., 2004. Tuning curves for approximate numerosity in the human intraparietal sulcus. Neuron, 44 (3), 547–555, with permission from Elsevier, and nidopallium caudolateral in the crow reprinted by permission from Macmillan Publishers Ltd. (Nature); Nieder, A., 2016. The neuronal code for number. Nat. Rev. Neurosci., Copyright (2016).)

lever if the arrays had the same number of items and held the lever if they did not. Using single cell recording, researchers found that individual neurons in the IPS as well as areas within the prefrontal cortex fired selectively for specific numerical values. Similarly, studies using fMRI have shown that parallel regions in the IPS and prefrontal cortex are activated during number comparisons in human adults and children (Ansari, 2008; Cantlon et al., 2006; Piazza et al., 2004; Lussier and Cantlon, 2016). Those results suggest homologous neural functions between humans and monkeys for numerical processing. Evidence showing that functional homologies between humans and monkeys in the IPS extend to many other neural functions also is consistent with the interpretation of neural homology in numerical processes (Orban et al., 2004).

Although there is no homologous structure to the IPS in the avian brain, neural recordings from crows reveal the same neural signatures of the approximate number representation within an analogous structure to the primate neocortex (the nidopallium caudolateral; Güntürkün, 2005; Ditz and Nieder, 2015). Neurons within the nidopallium caudolateral fire selectively for specific numerical values and their firing rate decreases as the number presented gets farther from their preferred value. This neural firing pattern is similar to neural responses in primates; however, the underlying neural structure is functionally and anatomically distinct (Ditz and Nieder, 2015). These findings from birds suggest that there are at least two highly similar yet independently evolved solutions to numerical representation in the animal kingdom (Nieder, 2016). It is thus possible that cognitive and neural processes accomplish numerical representation with similar signatures but evolved independently. A proper phylogenetic analysis of the evolution of numerical abilities could provide additional insights as into whether other species evolved these abilities from common or independent origins (Northcutt and Kaas, 1995; Sereno and Tootell, 2005).

3.27.7 Conclusion

Human numerical perception is shared with many other animal species and likely evolved early in our evolutionary history. Nonhuman animals and preverbal children can use this evolutionarily primitive ability to represent number directly and abstractly, across different sensory modalities, and over space and time. Nonhuman animals use this ability spontaneously in a variety of foraging and social interactions, which likely aids in survival. Current evidence from cognitive and neural comparisons between humans and monkeys implicate a common evolutionary origin for numerical representations in primates. Both humans and monkeys show signatures of Weber's law during cognitive comparisons of numerosities, and both show numerosity-specific neural tuning within the IPS during quantitative tasks. Thus, although other species may have evolved a similar representational system independently, current evidence suggests homologous evolution of numerical cognition in primates. Primate representations of numerosity are influenced by both the maturation rate of the species and experience with numerical discrimination. Humans have a slow maturation rate, and therefore a comparatively slow time course for developing numerical competency. However, humans' number acuity eventually reaches much more precise levels than that of nonhuman animals. This is likely due to the cultural influences of formal mathematics training on the primitive number system. Taken together, this research provides strong evidence that evolutionary constraints impact the development of human numerical cognition. Evolutionary constraints are thus at the foundation of human mathematics development.

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