Primitive Concepts of Number and the Developing Human Brain

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ABSTRACT

Counting is an evolutionarily recent cultural invention of the human species. In order for humans to have conceived of counting in the first place, certain representational and logical abilities must have already been in place. The focus of this article is the origins and nature of those fundamental mechanisms that promoted the emergence of the human number concept. Five claims are presented that support an evolutionary view of numerical development: (1) number is an abstract concept with an innate basis in humans; (2) maturational processes constrain the development of humans' numerical representations between infancy and adulthood; (3) there is evolutionary continuity in the neural processes of numerical cognition in primates; (4) primitive logical abilities support verbal counting development in humans; and (5) primitive neural processes provide the foundation for symbolic numerical development in the human brain. We support these claims by examining current evidence from animal cognition, child development, and human brain function. The data show that at the basis of human numerical concepts are primitive perceptual and logical mechanisms that have evolutionary homologs in other primates and form the basis of numerical development in the human brain. In the final section of this article, we discuss some hypotheses for what makes human numerical reasoning unique by drawing on evidence from human and non-human primate neuroimaging research.

Number is an abstract concept with an innate basis in humans

Number is an abstract quantitative representation that cuts across sensory modalities and 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 numerosity in nature. Sets that have a greater number of objects are often more dense, have a higher rate or greater duration, and take up more space or surface area. Some have argued that these dimensions are the earliest building blocks of quantitative representation in human infants (Gebuis & Reynvoet, 2011; Lourenco & Longo, 2011; Mix, Huttenlocher, & Levine, 2002a; Walsh, 2003). However, many of these non-numerical 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, numerosity is a quantitative dimension that can be represented in any sensory modality. Unlike rate (temporal) or density (spatial), a numerical sum can be calculated from objects distributed across 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. Number is, in principle, a truly amodal concept—akin to dimensions such as spatial distance or temporal duration.

There is evidence that an amodal concept of number is a fundamental component of human and animal cognition (Spelke, 2000; Spelke & Kinzler, 2007). Crossmodal numerical representation has been observed in non-human animals such as rats and monkeys (Jordan, MacLean, & Brannon, 2008; Meck & Church, 1984). In one study, rats were trained to press one lever after hearing 2 tones or seeing 2 lights and a second lever after hearing 4 tones or seeing 4 lights. When those rats were subsequently tested with a compound sequence of 2 tones and 2 lights, they spontaneously summed the items and pressed the lever associated with 4 items (Church & Meck, 1984). Jordan et al. (2008) showed that monkeys can numerically match and tally sets across modalities by comparing and summing auditory and visual sets of 1–9 items. Monkeys who were presented with mixed sequences of visual shapes and auditory tones successfully chose the sum of the items from two choice arrays. Importantly, the study showed that the monkeys' representations were truly numerical and not based on alternative dimensions such as rate, duration, density, or surface area since those cues were uncorrelated between the sample stimuli and targets. The data from rats and monkeys conclusively show that non-human animals engage crossmodal representations during numerical judgments.

Human infants also show sensitivity to numerical values across modalities. In one study (Kobayashi, Hiraki, & Hasegawa, 2005), 6-month-old infants were familiarized with a display of two and three dolls sequentially impacting a surface and emitting a tone at impact. Infants were then tested with trials in which an occluder blocked the infant's view, and the infant only heard the impact sounds of two or three tones. Then the occluder was removed and two or three dolls were revealed. Infants looked significantly longer at the numerically non-matching outcomes, indicating they formed an expectation of the number objects they should see based on the number of tones they heard. In another looking time study, (Jordan & Brannon, 2006) showed that 7-month-old human infants and rhesus monkeys spontaneously match the number of entities they see with the number of events they hear when multiple individuals are shown vocalizing simultaneously. Izard, Sann, Spelke, and Streri (2009) showed that newborn human infants look longer at visual arrays that displayed the same number of items as sounds they heard in an auditory sequence compared to arrays with different numerosities—showing that they spontaneously associate the number of sounds they hear with the number of visual objects they see. Representations of alternative dimensions such as surface area or duration are unlikely to explain newborns' crossmodal number discrimination because that would require a priori associations among the values of different properties (e.g., density and rate) across modalities at birth.

In the crossmodal discrimination study by Izard and colleagues, the newborns looked longer at the congruent auditory-visual sets for 4 vs. 12 items and 6 vs. 18 items (3:1 ratio), but only marginally discriminated between 4 vs. 8 items (2:1 ratio). One important feature of primitive nonverbal numerical representations, and what distinguishes them from the precise representations of symbolic counting, is that they are analog approximations of numerical value (Xu & Spelke, 2000). In studies with infants and animals, discrimination of numerical values is constrained by *Weber's law*—as the ratio between the to-be-compared numerical values narrows, infants' and animals' discrimination of the values declines. Thus, infants and animals will perform better at discriminating numerosity at a wide ratio, 4 vs. 12 items and 6 vs. 18 items (3:1 ratio), than 4 vs. 8 items, a narrow ratio (2:1 ratio), and this prediction has been proven many times across studies with infants and animals (see Agrillo & Beran, 2013; Cantrell & Smith, 2013; for reviews). Ratio-dependent discrimination shows that infants and animals are only approximating numerical values and not counting precisely (Gallistel & Gelman, 1992; Wynn, 1990, 1992).

Older children and adults show ratio-dependent numerical performance when they are prevented from verbally counting (Barth, Kanwisher, & Spelke, 2003; Barth, La Mont, Lipton, & Spelke, 2005; Cantlon & Brannon, 2006; Cordes, Gelman, Gallistel, & Whalen, 2001; Halberda & Feigenson, 2008). When adults and 5-year-old children rapidly sum items across modalities without verbally counting they show the signature of Weber's law in their performance, just as is observed in nonverbal animals and human infants (Barth et al., 2003, 2005). Children and adults are less accurate at numerically discriminating sets of objects when the numerical ratio is narrow (e.g., 3:4) vs. wide (e.g.,

1:4). These findings show that even after symbolic counting develops, humans retain a fundamental ability to approximate numerical quantities across modalities. Ratio-dependent discrimination of numerical values occurs during nonverbal enumeration within- and between-modalities and is widespread across many animal species, and stages of human development (see Agrillo & Beran, 2013 for a review; Barnard et al., 2013; Beran, Decker, Schwartz, & Schultz, 2011; Cantlon & Brannon, 2006; Feigenson, Dehaene, & Spelke, 2004; Ferrigno, Hughes, & Cantlon, 2015; Hanus & Call, 2007; McCrink & Wynn, 2004; Rugani, Vallortigara, & Regolin, 2013).

Together, the data from human infants, children, and non-human animals show that numerical cognition has an innate and evolutionary basis in humans. The nature of the innate number concept is an abstract analog intensity representation that noisily approximates numerical values and is ratio-dependent in its implementation. This nonverbal representation of number in humans is referred to as "core knowledge" of number (Carey & Spelke, 1994; Spelke, 2000; Spelke & Kinzler, 2007).

Maturation constrains the early development of numerical representations

The dominant view of nonverbal numerical development is that there is continuity between infants' and children's core knowledge of number and adults' nonverbal numerical estimation abilities (e.g., Brannon, 2006; Dehaene, Molko, Cohen, & Wilson, 2004). As described, human infancy researchers have revealed nonverbal quantitative sensitivities in humans within the first year of life using implicit measures such as looking time (e.g., Cordes & Brannon, 2008; Izard et al., 2009; Lipton & Spelke, 2003; Xu & Spelke, 2000). By 3 years of age, children can perform explicit numerical tasks such as choosing the numerical match for a set of 8 dots from two choice arrays (Brannon & van de Walle, 2001; Cantlon, Fink, Safford, & Brannon, 2007; Huntley-Fenner, 2001; Huntley-Fenner & Cannon, 2000). The numerical representations that children use to make nonverbal quantitative choices are similar to those of human infants in that they are approximate and ratio-dependent. Children's discrimination of numerical quantity gradually improves between the ages of 3 years and adulthood (Halberda & Feigenson, 2008; Huntley-Fenner, 2001; Huntley-Fenner & Cannon, 2000). However, there is a gap in our understanding of nonverbal numerical development during the period from 12 months to 3 years (Brannon & van de Walle, 2001; Mix, Huttenlocher, & Levine, 2002b; Sella, Berteletti, Lucangeli, & Zorzi, 2016). One- to two-year-old children often fail explicit numerical comparison tasks with values larger than 3 or 4 items (Feigenson & Carey, 2005). These failures are a bit mysterious because it is unclear why 1- to 2-year-old children fail to make quantitative judgments over stimuli that infants can discriminate in looking time tasks. For example, 6- to 9-month-old infants are able to discriminate sets of 1 vs. 4, 2 vs. 4, and 5 vs. 10 in looking time tasks (Cordes & Brannon, 2008; McCrink & Wynn, 2004) whereas 1-year-olds often fail to crawl to the larger set of crackers in contrasts of 1 vs. 4, 2 vs. 4, and 5 vs. 10 (Feigenson & Carey, 2005; Feigenson, Carey, & Hauser, 2002; vanMarle & Wynn, 2011). Other researchers have found that 2- to 3-year-old children's abilities to make numerosity-based choices are limited and depend on the emergence of other cognitive skills (Brannon & van de Walle, 2001; Michie, 1985; Mix, 1999).

One explanation of toddler's numerical approximation failures is that during this age they use a mental model of set representations that is limited to only a few items ("object files"). Feigenson & Carey (2003, 2005) argue that toddlers represent sets as a collection of individual objects via an object tracking mechanism. The object file mental model has a capacity limit of around 4 items, which limits children to numerical comparisons of only small sets. This object-based representation causes toddlers to fail at large number discriminations that infants and older children succeed at making with sequentially and simultaneously presented sets. Thus, one explanation of 1- to 2-year-olds' unique failures at making numerical discriminations in explicit choice tasks is that they use a mental model of object sets that interferes with large number representation.

A second possibility is that that infants' successes and failures could be related to the regularity of quantitative information in the stimuli. Cantrell, Boyer, Cordes, and Smith (2015) found that infants

are better able to make numerical discriminations in looking time tasks when they are shown less variable exemplars of a given numerosity (e.g., narrow distribution of cumulative area and contour) compared to more variable exemplars (wide distribution of area and contour). They argue that signal clarity influences infants' sensitivity to number across tasks, and this explanation accounts for some patterns in the literature (Cantrell & Smith, 2013). However, the 'signal clarity hypothesis' does not explain why younger infants succeed with looking time but older children fail with explicit choice at comparisons of 1 vs. 4 and 2 vs. 4 when non-numerical dimensions are fully correlated with numerosity.

Another explanation of toddlers' failures at large number discrimination, potentially non-exclusive with the object file and signal clarity explanations, is that children's perceptual, attention, decision, and motor processes are constrained by maturational factors that must unfold before children can express accurate numerical choices. The main evidence that infants discriminate numerosities comes from looking time studies. Infants' looking behaviors might be driven by implicit exploratory processes that are distinct from those underlying the explicit decisions required in choice tasks. It is unclear how the representations that infants use to discriminate large numerosities in looking time studies become the numerical representations that 3- and 4-year-old children use to select the larger numerosity from a set of options. Infants and toddlers undergo significant changes in their abilities to integrate perceptual, attention, and decision processes with motor control processes during the first years of life (Diamond, 1990, 1991; Gomez, 2005; Smith & Thelen, 2003). The maturation of cognitive systems could play a role in the emergence of numerical choice in toddlers.

Research with infant monkeys supports the idea that maturational factors could play an important role in human numerical development. In the domains of physical growth, motor behavior, and perceptual development, monkeys mature much faster than humans. For instance, human infants begin to crawl around 9–10 months of age whereas monkey infants begin to crawl within 1 month of birth (Hinde & Spencer-Booth, 1967). Similarly, in terms of perceptual development, infant monkeys begin reaching for occluded objects by 4 months of age, where as human infants do not develop this ability until 9–12 months of age, a rate that is 2–3 times slower than infant monkeys (Diamond, 1990, 1991; Gomez, 2005). If quantitative development in human and non-human primates is constrained by the unfolding of genetically predetermined abilities, or maturation, then monkey infants should engage in quantitative judgments earlier than human infants. Alternatively, if the development of spontaneous quantitative reasoning of monkeys is related to learning then infant monkeys should perform worse than adult monkeys and learning rates should differ between age groups.

Recent data from infant monkeys show that numerical abilities develop rapidly in non-human primates. Infant monkeys make accurate quantity choices and the spontaneous quantitative sensitivity of infant monkeys is equal to that of their adult groupmates. Ferrigno et al. (2015) tested untrained infant and adult monkeys on a food quantity choice task and measured their first trial accuracy across a range of numerical comparisons from 1–9 items. The one-year-old infant monkeys performed above chance and at accuracy levels equivalent to the adult animals in their group (Figure 1; Ferrigno et al., 2015). Further, learning rates, the changes in accuracy over time, did not differ between infant and adult animals. Finally, infant monkeys accurately performed this numerical task with large numerical values at 1 year of age whereas human children at the same age often fail. One-year-old human children often fail to choose the larger of 1 vs. 4 and 2 vs. 4 treats and only show reliable success on this explicit choice task at a later age. The Weber fractions of 1-year-old monkeys ($w = .71$) were comparable to those of a 2- to 3-year-old human child (3-year-old mean $w = .53$ in Halberda & Feigenson, 2008). The results show that monkeys develop quantitative reasoning abilities 2 to 3 times faster than humans, which is similar to the accelerated rate of aspects of their perceptual and motor development regarded as genetically constrained (Diamond, 1990, 1991). Together, these findings implicate a maturational contribution to the development of numerical cognition in monkeys and humans. The development of numerical choice behavior appears to be yoked to the species' rate of maturation.
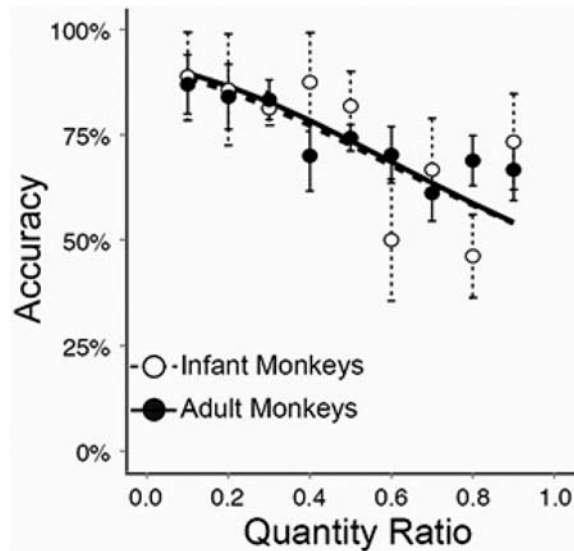
Figure 1. Adult and infant monkeys' accuracy as a function of quantity ratio (smaller quantity/larger quantity). Solid lines (adults) and dotted lines (infants) represent fits predicted by a model of Weber's law (Goodness-of-fit: Adults: $R^2 = .76$, $p < .01$, Infants: $R^2 = .50$, $p < .05$). Error bars represent the SE of the mean. From (Ferrigno et al., 2015).

Evidence that maturation affects numerical cognition does not imply that learning cannot alter quantitative reasoning. For instance, with training, adult monkeys' performance can improve to that of 4- to 5-year-old human children (Cantlon & Brannon, 2006). The data from infant monkeys highlight that quantitative reasoning is natural in primates, and a primary constraint on early numerical development is species' rate of maturation. The relatively slow pace of the development of explicit numerical judgment in human children is not necessarily caused by the need for extensive learning, as suggested by some researchers (Mix, 2002). Maturational factors could cause human children's difficulties comparing large quantities during their first two years (Ferrigno et al., 2015). Together the data from infants of both species suggest continuity in the development of numerical representation from infancy to adulthood—nonverbal numerical cognition has a strong innate basis and its subsequent development into a system of explicit choice is constrained by genetic maturation.

Evolutionary continuity in neural mechanisms

If numerical cognition has an innate basis in humans, derived from evolution, then there should be continuity in the neural mechanisms underlying numerical cognition between humans and other animals. Animals as different as bees, ants, various types of fish, salamanders, chickens, pigeons, crows, raccoons, rats, lions, bears, elephants, and primates make quantity discriminations (see Agrillo & Beran, 2013 for review). The many examples of quantitative and numerical reasoning in nature raise questions about whether those behaviors arise from a common evolutionary origin or are instead cases of convergent evolution. Comparisons of the neural structures that underlie numerical behaviors could be informative.

In monkeys who are trained to match visual arrays of dots based on number, single neurons along the intraparietal sulcus (IPS) will respond maximally to a preferred numerical value and their firing rate decreases as the number that is presented gets numerically farther from that preferred value (Figure 2; Nieder & Miller, 2004). In addition, neurons tuned to larger numerical values exhibit noisier responses than neurons tuned to smaller values (Nieder & Merten, 2007). That is, neurons tuned to larger numerical values have a coarser response and respond to a wider set of adjacent numerical values than
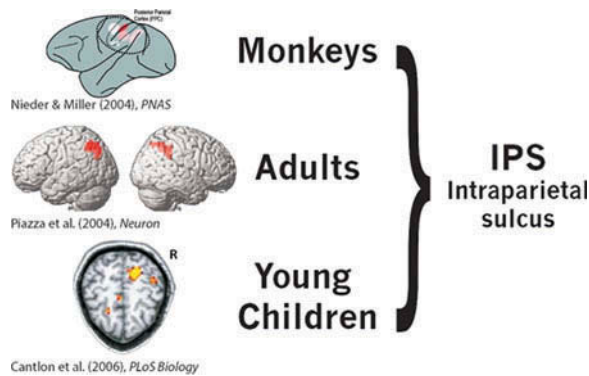
Figure 2. Monkeys, human adults, and human children exhibit similar activation in the intraparietal sulcus (IPS) during analog numerical processing. From Cantlon (2012).

neurons tuned to smaller values. The finding that neural responses in the IPS are modulated by both numerical distance and numerical magnitude represents a neural version of the numerical ratio effect, or Weber's law. A similar pattern of ratio-dependent numerical tuning has been observed with fMRI in the adult human IPS (Figure 2; Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004). During passive viewing adaptation, wherein adults show decreasing neural responses to a constant stimulus, the IPS responds more strongly to sudden changes in number (over shape) and the amount of numerical change modulates the change in the neural response in a ratio-dependent manner.

One study showed that the same neural region selective for numerical processing in monkeys and adult humans (the IPS) is selective for numerical value (over shape) in 4-year-old children (Figure 2; Cantlon, Brannon, Carter, & Pelphrey, 2006). This suggests that numerical processing in the IPS is a developmentally primitive neural phenomenon. EEG and NIRS studies with infants do not offer the same spatial localization capacity as fMRI but those studies are also consistent with this conclusion (Hyde, Boas, Blair, & Carey, 2010; Hyde & Spelke, 2011; Izard, Dehaene-Lambertz, & Dehaene, 2008; Libertus, Brannon, & Woldorff, 2011; Libertus, Pruitt, Woldorff, & Brannon, 2009). They suggest that by as early as 3 months of age infants show number-specific parietal responses to nonverbal stimuli such as sets of objects. fMRI studies with older children confirm that nonsymbolic numerical representations maintain a connection with the neural processes of the IPS throughout development (Ansari & Dhital, 2006; Cantlon et al., 2009; Lussier & Cantlon, 2016). These findings implicate early-developing and homologous neural mechanisms in the IPS between humans and monkeys as a source for numerical processing. Evidence of functional homologies between the human and monkey IPS from other cognitive domains also support the claim of neural homology in numerical processing in primates (Orban et al., 2006).

Although there is no homologous structure to the IPS in the avian brain, neural recordings from crows reveal similar neural signatures of approximate number representation within an analogous structure to the primate neocortex: the nidopallium caudolaterale (Figure 3; Ditz & Nieder, 2015; Güntürkün, 2005). Neurons within the nidopallium caudolaterale 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 & Nieder, 2015). These findings from birds show 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 mechanisms, but evolved independently. The numerical abilities of fish, insects, birds, reptiles, amphibians, and some mammals may also show similar numerical processes that evolved independently from humans and other primates. A proper phylogenetic analysis of the evolution of numerical abilities could provide additional insights as to whether other species evolved numerical abilities from common or independent origins (Northcutt & Kaas, 1995; Sereno &
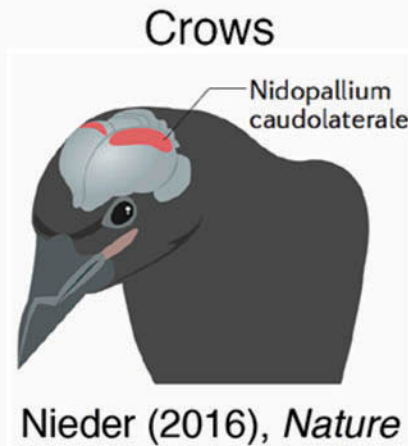
Figure 3. The neural representation of number in corvids is observed in the nidopallium caudolaterale, a region that has no clear homolog in primates. From (Nieder, 2016).

Tootell, 2005). So far, the evidence suggests evolutionary continuity between the numerical processes of humans and other primates, and analogous numerical processes in avian species.

Primitive numerical logic supports human counting development

Unlike nonhuman primates and other animals, humans eventually develop the unique ability to represent numbers exactly with symbols such as words and numerals. In contrast to the nonverbal number system, which represents numerical quantity imprecisely, a symbolic number is represented with complete precision. An open question is how and when representations of symbolic number are supported by the primitive, nonverbal, approximate number system.

The *symbol grounding problem* in numerical cognition explores how we attach meaning to arbitrary shapes or sounds with values. For instance, the numeral "4" and the spoken word "four" are in no way intuitively suggestive of a particular quantity and thus, must be grounded in a more fundamental type of numerical representation. This raises the question of how humans develop the ability to map symbolic numbers onto nonverbal representations. To answer this question, developmental researchers have studied the changes in numerical cognition that occur during early childhood when children are learning to count and to link number words to particular quantities.

Counting acquisition is a lengthy and difficult process for children. They begin by learning to rote recite the count list, but it is not until months or years later that children begin to understand that the words in the count list refer to specific, exact quantities (Le Corre & Carey, 2007; Wynn, 1990, 1992). For instance, even if a child can recite the count list to 10, until they are approximately 2.5 years old, they may not correctly produce one item when asked for just one item. Even then, despite producing one item when asked for one, they will continue to produce a random handful of objects for any quantity larger than 1. Over the next 6–12 months, children go through stages in which they are able to correctly produce 2 objects, then 3 objects, and then 4 objects. After this point, when children can correctly produce 5 or 6 objects, they are labeled as Cardinality Principle (CP)-knowers, meaning that they understand that when counting a set of items, the number word that they end on represents the number of items in the set (Gelman & Gallistel, 1978; Wynn, 1990, 1992). This principle allows children to understand that number words beyond the highest number they can count to (i.e., beyond their count list) refer to unique quantities, that stirring or shaking a large set of items does not change

the cardinality of the set, that removing one item or adding an item changes the cardinality of the set, and that returning the same or a different item after removing one item does not change the set's cardinality (Lipton & Spelke, 2006).

Although there is some debate as to how representations for the first four number words are grounded (see Le Corre & Carey, 2007; Odic, Le Corre, & Halberda, 2015), researchers agree that number words are, at some point in development, mapped to approximate numerical representations, potentially via structural alignment (Carey, 2004, 2009; Gentner, 2010). One debate in the field concerns when this mapping occurs. Older work suggests that the mapping between symbolic number and nonsymbolic number does not occur until after children learn to count. Le Corre and Carey (2007) found that children who were not yet CP-knowers, and even some children who were CP-knowers, could not accurately apply a number word to label large arrays of dots. That is, they applied similar verbal estimates for arrays of 5 dots and arrays of 9 dots rather than using smaller number words for the 5-dot arrays and larger number words for the 9-dot arrays. From this they concluded that children do not map number words to approximate number representations until sometime after acquiring the counting principles. Instead, they argued that early counters rely on "object file" representations of small sets to map the meanings of the first few count words. A related study found that children could correctly give an approximate number label for quantities within their count list, but unskilled counters, who could not correctly transition between decade changes (e.g., could not produce 80 after 77, 78, 79), could not make correct approximations beyond numbers in their count list (Lipton & Spelke, 2005). This further suggests that children do not map approximate quantities to number words until they are proficient at counting (Lee & Sarnecka, 2011).

In contrast, other newer work finds that when children are asked to physically produce a specific number of items, even children who have not yet mastered the cardinality principle can approximately provide the correct number of items and tend to give more items for larger number words (Gunderson, Spaepen, & Levine, 2015; Wagner & Johnson, 2011). This suggests that children do map symbolic to nonsymbolic representations prior to mastering the counting principles. One possibility that might reconcile conflicting accounts is that mapping is asymmetric, that is, children may learn to map from quantities to number words later than mapping from number words to quantities. To test this prediction, Odic et al. (2015) tested the same group of children on their ability to map both quantities to number words and number words to quantities. They found that children were unable to map quantities to number words until after they had acquired the counting principles, but could map number words to quantities prior to counting. Thus, they suggest that mapping between the approximate number system and exact, symbolic number might be asymmetric—mapping from exact to approximate number could develop earlier than the mapping from approximate to exact representations (see also Mundy & Gilmore, 2009; Opfer, Thompson, & Furlong, 2010). However, one important consideration is that Gelman (1993) showed that task competence is a critical factor in eliciting systematic counting behavior in young children. Therefore, some of the inconsistencies in the literature may be due to differences in task demands rather than asymmetries.

Most research on counting development has focused on this issue of how the mappings between representations in the nonsymbolic and symbolic number systems emerge, and whether those mappings help children learn to count. As discussed above, there is a debate over this issue and it is still unclear whether the mapping of count words to nonverbal numerosity representations plays a causal role in counting acquisition. However, the mapping of representations is only one small possibility for a fundamental link between the symbolic and approximate number systems (Gallistel & Gelman, 2000). Another source of continuity between the nonsymbolic and symbolic numerical systems could be in the logical algorithms of the approximate number system and how those mechanisms could provide structure for counting acquisition (Cantlon, Piantadosi, Ferrigno, Hughes, & Barnard, 2015; Gallistel & Gelman, 1992; Gelman, 1990).

Gelman (1990) and Gallistel (Gallistel & Gelman, 1992; Gelman & Gallistel, 1978) proposed a set of implicit logical principles inherent in nonsymbolic numerical estimation that structure the verbal

counting routine during development. The principles include one-to-one correspondence between each set item and the internal quantity representation, and sequential composition wherein the internal quantity representation is assembled by first passing through smaller values en route to the cardinal value. There is some support that "first principles" are primitive components of numerical reasoning in human children and non-human primates. Evidence of spontaneous "protocounting" behavior in non-human primates and evidence of pre-counting 1-to-1 correspondence judgments in human children support the argument that nonsymbolic counting adheres to logical principles that subsequently emerge in verbal counting.

One logical algorithm by which symbolic counting and approximate numerical systems are similar is iterative comparison. A recent study found that non-human primates possess logic for comparing quantities in sequence, item-by-item, that is algorithmically similar to human counting (Cantlon et al., 2015). Monkeys were given the task of choosing between two food caches. Monkeys saw one cache (Set 1) baited with some number of food items, one item at a time. Then, a second cache (Set 2) was baited with food items, one at a time. At the point when the second set approximately outnumbered the first set, monkeys spontaneously moved to choose the second set even before it was completely baited. As shown in Figure 4, monkeys mostly switched when the difference of Set 2-Set 1 was greater than zero—that is, when the second set began to outnumber the first set. A series of control conditions showed that the monkeys' switching behavior was based on numerosity rather than duration or other cues. The monkeys' behavior was tested against the predictions of a counting-like process wherein every time an item was added to Set 2, the monkeys (a) incremented their mental representation of the value of the set, (b) executed a mental comparison between Set 1 and Set 2, (c) checked whether Set 2 was greater than or equal to Set 1, and (d) terminated the comparison routine and committed to choose Set 2 when Set 2 was approximately equal to or greater than Set 1. This "protocounting" model provided a valid explanation of the monkeys' behavior with the caveat that the monkeys' representations of the numerical values of the sets included scalar noise that resulted in approximate numerical representations rather than precise representations. Thus, the monkeys used a noisy counting-like algorithm that is logically parallel to human counting. The major implication of this research is that a set of core algorithmic operations, rooted in nonverbal quantity representation, preceded the emergence of verbal counting in human cultural evolution.
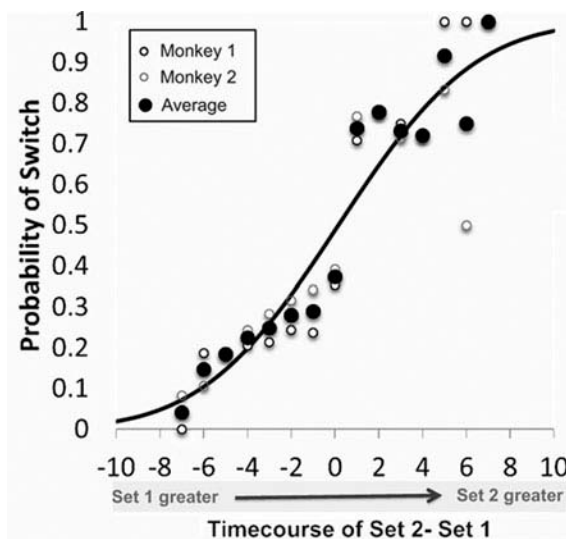

Figure 4. Probability of a switch behavior. Monkeys were increasingly likely to switch to Set 2 as the difference between Set 1 and Set 2 approached zero and the value of Set 2 began to exceed that of Set 1. From (Cantlon et al., 2015).

Another logical algorithm that emerges in children's early quantitative behavior is one-to-one correspondence (Izard, Streri, & Spelke, 2014; Mix, 2002). In Izard et al. (2014), two-and-a-half-year-old children were presented with a set of finger puppets placed in one-to-one correspondence with the branches of a tree toy. On each trial, the puppets were taken from the branches and placed in an opaque box. Children were allowed to search the box to retrieve either all the puppets, or all but one puppet. Children's representation of the number of puppets in each condition was indexed by the time they spent searching the box for more puppets. Sets of six items were presented and children were unable to verbally count that high. The results showed that children could discriminate 5 vs. 6 using the one-to-one correspondence relation—they searched longer when all but 1 item had been retrieved from the box compared to when all items were retrieved. Children failed to search longer for the missing item when the one-to-one relation was either disrupted (e.g., by having more branches than puppets) or less transparent (e.g., adding or subtracting items from the box). The data show that children have some (albeit weak) routine for measuring numerical value using the principle of one-to-one correspondence.

Evidence from cross-notation mapping studies with children who are in the process of acquiring counting, and studies of the principles governing nonverbal quantitative judgments in animals and infants suggest a structural relation between the logic of nonsymbolic number computation and verbal counting. The structure of preverbal numerical cognition, and its logical algorithms, could provide support for the acquisition of human counting and computation in children—an issue of on-going study. The general argument in favor of a structural dependency between preverbal and verbal counting logic is that nonverbal models and logical algorithms are necessary precursors in order for children to interpret the verbal reference and learn to count (Gallistel & Gelman, 1992). Further evidence is needed for a full explanation of the types of nonverbal models that children use to make sense of counting and the causal relations among different representational systems (Carey, 2009). The principles of nonverbal numerical representation could provide structure for the acquisition of the verbal counting routine, even if those routines ultimately diverge into different mechanisms with different output representations. At a minimum, evidence of shared logical rules between nonverbal "protocounting" and verbal counting suggests an evolutionary relation between the systems.

Primitive neural processes provide the foundation for symbolic numerical development in the brain

If there is a relation between symbolic and nonsymbolic numerical processes then there should be a physical relation between those processes in the brain. The parietal lobe, and specifically the IPS, is widely known to be involved in both symbolic and nonsymbolic number processing in human adults and children (e.g., Ansari & Dhital, 2006; Ansari, Dhital, & Siong, 2006; Ansari, Garcia, Lucas, Hamon, & Dhital, 2005, 2006; Cantlon et al., 2009; Eger, Sterzer, Russ, Giraud, & Kleinschmidt, 2003; Evans et al., 2015; Menon, Rivera, White, Glover, & Reiss, 2000; Piazza et al., 2004, 2007; Pinel, Piazza, Le Bihan, & Dehaene, 2004; Rivera, Reiss, Eckert, & Menon, 2005; Vogel, Goffin, & Ansari, 2015).

One approach for determining whether children's primitive numerosity representations are a source for symbolic numerical learning is to ask whether there is functional overlap between nonverbal numerical representations and symbolic numerical representations in the brain during development. Biological approaches to the symbol grounding problem propose that neural mechanisms that underlie a more primitive aspect of numerical cognition (i.e., approximate numerical representations) will support the development of the more evolutionarily recent abilities (i.e., symbolic number). This would be consistent with the idea of exaptation in evolutionary theory (Gould & Vrba, 1982) wherein neural processes take on new functions that are derived from their prior functions (Dehaene & Cohen, 2007).

Over several studies researchers showed that the neural regions young children use for nonverbal numerical processing substantially overlap with those they engage during symbolic numerical

processing of digits and words (e.g., Cantlon et al., 2009; Holloway & Ansari, 2010; Lussier & Cantlon, 2016). Functionally similar and anatomically overlapping patterns of IPS activation are observed for numerical processing of digits, dots, and number words in children ranging in age from 4 to 8 years, even when activation from a variety of different control tasks is subtracted (Figure 5). In addition, Holloway and Ansari (2010) reported functional overlap between symbolic (digits) and nonsymbolic numerical responses in the IPS in 7- to 8-year-old children. Together these data show neural continuity between the neural processes underlying nonverbal numerical cognition and those of symbolic numerical cognition. The findings suggest that there is at least a functional relation between these neural processes such that they occupy common substrates, and further suggest the possibility of a developmental dependency relation wherein children construct formal numerical concepts by drawing on the mechanisms of nonverbal numerical representation.

Additional evidence in support of a developmental relation between nonverbal numerical cognition and symbolic number comes from research on individual differences in the brain and behavior (Ansari, 2008; de Smedt, Noël, Gilmore, & Ansari, 2013; Halberda & Feigenson, 2008; van Marle, Chu, Li, & Geary, 2014). If children's approximate, nonverbal numerical representations are related to their precise, symbolic numerical concepts, then their neural responses during approximation should predict how well they learn symbolic number concepts. Although this has not yet been experimentally tested, Bugden, Price, McLean, and Ansari (2012) showed that symbolic number-modulated activity in the left IPS, which is also involved in processing nonsymbolic number, is related to arithmetic fluency in 8–10-year-old children (controlling for general factors). There is also longitudinal evidence that number-related activation in the left IPS from a cross-notation task predicts 4- to 8-year-old children's formal mathematics knowledge (controlling for general factors; Emerson & Cantlon, 2014). In addition, an IPS-based network involved in numerical approximation shows individual differences in functional connectivity that predict young children's mathematics knowledge (Emerson & Cantlon, 2012). Finally, the maturity of children's neural responses in the left and right IPS during natural viewing of educational videos is related to their mathematics knowledge, controlling for verbal knowledge (Cantlon & Li, 2013). The relation between children's neural maturity and mathematics ability overlaps children's neural activation to numerosity-to-digit comparisons in the IPS. Together these studies suggest a relation between the developmental trajectories of primitive numerical mechanisms and symbolic numerical knowledge over development.

Claims of neural overlap between the symbolic and nonsymbolic number systems do not imply that these systems are identical. The symbolic and nonsymbolic number systems are quite distinct. As discussed earlier, one system is approximate whereas the other is precise. Also, one system is partly built by language (symbolic) and the other system exists independently of language (nonsymbolic). We should expect to see differences at the behavioral level in how these systems develop, such as differences in the pace of their developmental trajectories. Evidence for such differences comes from individual differences studies showing that the developmental trajectories of symbolic and nonsymbolic numerical ability are not correlated for all tasks at all ages (de Smedt et al., 2013). Given the conceptual and computational differences
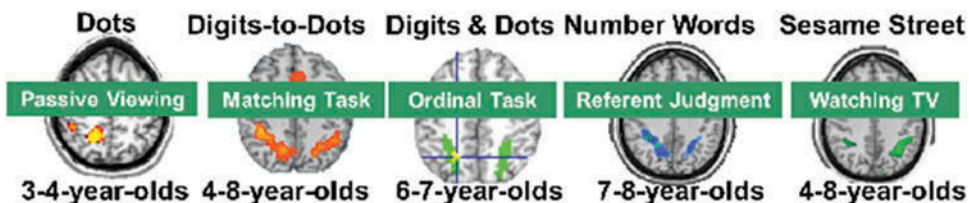
Figure 5. Human children engage the IPS during numerical tasks across a range of ages (from 4–8 years), tasks (Passive Viewing, Matching, Ordinal Comparison, Referent Judgment, and Watching TV), and numerical notations (visual arrays of dots, Arabic numerals, number words, and complex naturalistic input such as Sesame Street). Data are from (left to right): (Cantlon et al., 2006; Emerson & Cantlon, 2012; 2014; Cantlon et al., 2009; Lussier & Cantlon, 2016; Cantlon & Li, 2013).

between the symbolic and nonsymbolic number systems, we also should expect to see significant differences between the neural representations of symbolic and nonsymbolic numbers throughout the brain, especially as the symbolic system matures—and there is evidence for that too. Adults show regions of non-overlap between symbolic and nonsymbolic numerical representation in the intraparietal sulcus (Cohen Kadosh, Cohen Kadosh, Kaas, Henik, & Goebel, 2007) and throughout the brain (Bulthé, de Smedt, & Op de Beeck, 2014). We should additionally expect to see different patterns of functional connectivity between symbolic representations and the rest of the brain compared to nonsymbolic representations because symbolic numbers are associated with rote memorization procedures (e.g., arithmetic strategies), semantic information (e.g., phone numbers), and cultural systems (e.g., calendars, games, music) that nonsymbolic number representations are likely not. To date there has been no test of this last prediction.

Despite all of the potential to observe differences between symbolic and nonsymbolic numerical systems in the brain, we see a significant degree of continuity in their neural representations throughout development. At a minimum, the links between the numerical processes of the IPS in monkeys and humans, and symbolic and nonsymbolic numerical cognition implicate an evolutionary relation between primitive and culturally recent cognition (Dehaene & Cohen, 2007). Thus far, the neural evidence suggests that this evolutionary foundation provides input to children's developing numerical concepts. These data align with the data from behavioral development described earlier, which suggest a representational and logical relation between nonsymbolic numerical representations and symbolic number concepts.

Uniquely human numerical processing

Research, like that described in the previous section, suggests that the evolutionarily recent ability to represent symbolic number in humans is exapted from the more primitive ability to conceive of numerical quantity nonsymbolically (Dehaene & Cohen, 2007; Gould & Vrba, 1982). However, adult human numerical representations are unique and sophisticated beyond the primitive representations of monkeys and the immature representations of pre-counting and pre-literate children. Adult humans have exact ordinal representations of numbers, and they understand the logical properties of numbers in ways that non-human animals and young children do not (Boysen & Hallberg, 2000; Carey, 2009). For example, the successor function in verbal counting allows adults to recognize that adding one item to a set yields a cardinal value of the next item in the count list. Young children take years of numerical training to recognize the successor function of verbal counting (Carey, 2009; Wynn, 1992) and non-human animals never spontaneously learn the successor function even after years of numerical training (Biro & Matsuzawa, 1999, 2008; Murofushi, 1997; Tomonaga, 2008; but see Pepperberg & Carey, 2012).

Evidence for how human brain function is unique compared to non-human primates' and how adult brain function is unique compared to children's is extremely limited. However, some early evidence suggests that numerical processing in humans engages unique neural substrates compared to non-human primates. A recent fMRI study comparing neural activation to tone sequences in monkeys and humans showed that both groups engaged the IPS during numerical processing of the sequences but that inferior frontal cortex (BA 44/45) was engaged by humans to an extent not observed non-human primates (Figure 6; Wang, Uhrig, Jarraya, & Dehaene, 2015). Adult humans showed greater activation in regions of the inferior frontal gyrus than macaques when a novel number of tones was presented following passive adaptation to tone sequences with a constant number of tones. Adults further showed conjunctive activation in this same inferior frontal region when a tone sequence varied in pitch pattern from a standard sequence whereas macaques did not exhibit such activation. The authors relate these unique functions of the inferior frontal cortex in humans to language evolution. Although previous research has shown that prefrontal regions represent numerical categories in non-human primates (Nieder & Miller, 2003), these comparative fMRI data suggest that prefrontal cortex could play a unique role in integrating numerical
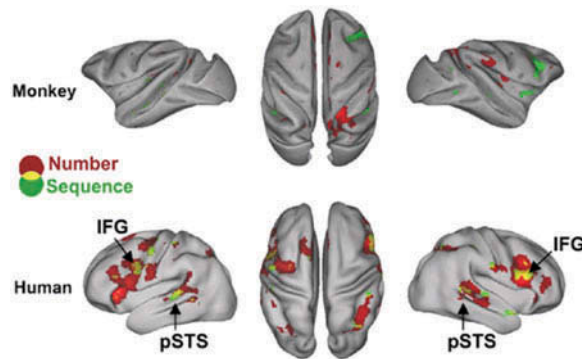
Figure 6. Monkeys (top) and humans (bottom) were tested during fMRI while they passively listened to sequences of tones that typically had the same number and pitch pattern. When deviant stimuli were presented monkeys and humans showed neural responses to the numerical changes (red) in the IPS and to pattern changes (green) in the IFG but only humans showed neural responses to numerical deviants in the IFG, overlapping IFG regions that responded to pattern changes (yellow). From Wang et al. (2015).

representations with sequence representations in humans—a function important for counting acquisition and symbolic numerical cognition.

Language (i.e., number words) plays a key role in linking symbols to nonverbal representations of number in humans, leading several researchers to argue that brain regions involved in processing semantic and linguistic relations, such as the prefrontal cortex, should be involved in developing the association between symbolic and nonsymbolic number representations (Cantlon et al., 2009; Nieder, 2009; Piazza et al., 2007). Some support for this hypothesis comes from work with symbol-trained nonhuman primates. Diester and Nieder (2007) trained monkeys to associate Arabic numerals with their values in sets of objects. After monkeys were trained to associate nonsymbolic dot arrays with symbolic Arabic numerals, neurons in both the IPS and prefrontal cortex represented the numerical values of the stimuli but the neurons in the prefrontal cortex were unique from those in the IPS because they more often responded equally to nonsymbolic and symbolic presentations of a particular numerical value, suggesting that associations between the symbolic and nonsymbolic number emerge in the prefrontal cortex (Diester & Nieder, 2007).

Many human neuroimaging studies of numerical processing have found recruitment of frontal regions in children to a degree that is not observed in adults (Ansari et al., 2005; Cantlon et al., 2009; Emerson & Cantlon, 2012, 2014; Holloway & Ansari, 2010; Lussier & Cantlon, 2016; Lyons & Ansari, 2009; Rivera et al., 2005). Three particular frontal loci emerge across neuroimaging studies of numerical cognition: a region of the inferior frontal gyrus bordering insular cortex, dorsolateral prefrontal cortex, and a region of anterior cingulate cortex. These regions tend to show stronger activation during numerical tasks compared to control tasks, and stronger activation in children compared to adults. The functions of these regions, and their role in symbolic vs. nonsymbolic numerical processing, and childhood vs. adulthood have multiple interpretations. Nonetheless, these regions, particularly the inferior frontal and dorsolateral prefrontal loci, are candidates for the language-based integrative functions of numerical processing that are unique to humans (Bookheimer, 2002; Vigneau et al., 2006).

Here we provide a summary of patterns of activation observed across fMRI studies of numerical development in symbolic vs. nonsymbolic tasks and in children vs. adults. We used meta-analytic tools to distill a pattern of cortical activation across 14 published neuroimaging studies of basic numerical processing in children. We discuss the patterns of activation observed between age groups and numerical notations as they relate to hypotheses about the functional demands of symbolic numerical cognition.

We identified 18 published empirical articles that tested basic numerical processing in children (only comparison or passive viewing tasks were included; see Table 1). The articles were identified using literature searches and cited reference searches in Web of Science. Several additional articles

Table 1. Summary statistics for each study included in the meta-analysis.

Authors	Year	Adult Info: Mean age (age range), Number of participants	Child Info: Mean age (age range), Number of participants	Numerical Task	Number Stimuli	Notation
Ansari et al.	2005	19.8 yr (19.1–21.1), n = 12	10.4 yr (9.2–11.1), n = 12	Magnitude Comparison	Arabic Numerals	Symbolic
Ansari & Dhital	2006	19.8 yr (18.8–21.1), n = 9	10.4 yr (9.1–11.1), n = 9	Magnitude Comparison	Square (dot) Arrays	Nonsymbolic
Cantlon et al.	2006	25 yr (21–37), n = 12	4.75 yr (4.25–4.95), n = 8	Adaptation	Dot Arrays	Nonsymbolic
Kaufmann et al.	2006	NA	9.6 yr, 8–12, n = 12	Magnitude Comparison (Number and Size)	Arabic Numerals	Symbolic
Cantlon et al.	2009	24 yr, n = 14	7.2 yr (6–8), n = 14	Magnitude Comparison	Dot Arrays & Arabic Numerals	Symbolic & Nonsymbolic
Kovas et al. **	2009	NA	10 yr, n = 26	Magnitude Comparison	Dot Arrays	Nonsymbolic
Wood et al.	2009	29.5 yr (23–40), n = 11; 68.1 yr (59–81), n = 9	9.4 yr (8–12), n = 10	Magnitude Comparison (Number and Size)	Arabic Numerals	Symbolic
Holloway & Ansari **	2010	23.5 yr (18.4–28.3), n = 19	8.25 yr (6.8–9.3), n = 19	Magnitude Comparison	Square (dot) Arrays & Arabic Numerals	Symbolic & Nonsymbolic
Meintjes et al.	2010	NA	10.5 yr (8.2–12.6), n = 16	Parity Judgment: which of two numbers is closer to a third	Arabic Numerals	Symbolic
Bugden et al.	2012	NA	8.8 yr (8–10), n = 17	Magnitude Comparison	Arabic Numerals	Symbolic
Emerson & Cantlon	2012	20.7 yr (18.9–25.4), n = 20	8.24 yr (4.3–11.9), n = 24	Cross-Notation Matching	Dot Array & Arabic Numerals Simultaneously	Cross-Notation
Cantlon & Li	2013	NA*	7.1 yr (4.3–10.8), n = 23	Cross-Notation Matching	Dot Array & Arabic Numerals Simultaneously	Cross-Notation
Mussolin et al. **	2013	NA	10.5 yr (8–14), n = 19	Magnitude Comparison	Arabic Numerals	Symbolic
Emerson & Cantlon	2014	20.7 yr (18.9–25.4), n = 20	6.6 yr (4.5–9.1), n = 17	Cross-Notation Matching	Dot Array & Arabic Numerals Simultaneously	Cross-Notation
Park, Li, & Brannon	2014	NA	5.6 yr (4.8–6.6), n = 21	Comparison—which is bigger	Dot Arrays & Arabic Numerals	Symbolic & Nonsymbolic
Haist et al. **	2015	22.4 yr (18–34), n = 16	9.8 yr (6–12), n = 14; 15.4 yr (13–17), n = 14	Magnitude Comparison	Dot Arrays	Nonsymbolic
Vogel, Goffin, & Ansari	2015	NA	10.2 yr (6–14), n = 19	Adaptation	Numerals	Symbolic
Lussier & Cantlon	2016	20.9 yr (18.2–23.3), n = 20	8.6 yr (8–9), n = 24	Nonsymbolic Magnitude Comparison; Symbolic Magnitude Comparison; Symbolic Categorization (Even or Odd)	Dot Arrays & Number Words (separate tasks)	Symbolic & Nonsymbolic

Note. *denotes a study that included adult participants, but not in the paradigm from which we draw peak coordinates.
**denotes a study that included points that were derived by comparisons with age or behavior and are not represented in the final meta-analysis.

that originally were identified by our search ultimately were excluded because they were written in a foreign language (n = 2, Russian: Varga, Pavlova, & Nosova, 2008; German: Krick et al., 2015), focused on a special population (children born prematurely, n = 1 Starke et al., 2013), reported results that were restricted by either another task or an anatomical mask (n = 2, Berteletti, Man, & Booth, 2014; Krinzinger et al., 2011), or had stimuli that were ambiguously symbolic or nonsymbolic (fingers; n = 1, Kaufmann et al., 2008). For each of the 14 included studies, we extracted the peak coordinates from all whole-brain analyses that localized numerical processing regions. This resulted in 163 sets of coordinates. All coordinates were converted to Talairach space. We included both the child and adult data in our analyses. Peaks that corresponded to whole-brain analyses that showed a relation between numerical processing and either age or a behaviorally obtained measure of numerical processing (e.g., numerical acuity or math achievement) were not included in the meta-analysis (peaks from n = 4 articles), but were consulted for consistency in interpreting the results of the analysis.

We conducted an activation likelihood estimation (ALE) analysis on all 163 points using GingerALE software (version 2.3.6, Eickhoff, Bzdok, Laird, Kurth, & Fox, 2012; Eickhoff et al., 2009; Turkeltaub et al., 2012). An ALE takes foci from various studies as input and calculates the likelihood of a particular region being recruited across studies. First, Gaussian blurs were applied to the foci such that studies with larger sample sizes were blurred with taller and tighter Gaussian functions, indicating greater confidence in those points than points derived from smaller samples. Modeled activation maps were then calculated by finding the maximum across the foci's Gaussians (Turkeltaub et al., 2012). The union of these modeled activation maps is the final ALE image. The probability of finding each value in a map is then calculated by making a histogram of the values in the modeled activation map and dividing by the number of voxels in the modeled activation map. The likelihood maps presented here were set to an uncorrected minimum thresholds of $p < 0.01$ (Figure 7, dark colors) and $p < 0.001$ (Figure 7, light colors) before applying a cluster correction to obtain a cluster level threshold of $p < 0.05$. Foci that were identified in their source publication by taking the conjunction of the neural response to symbolic and nonsymbolic stimuli were included in both the symbolic and nonsymbolic maps because they indicate a significant response to both types
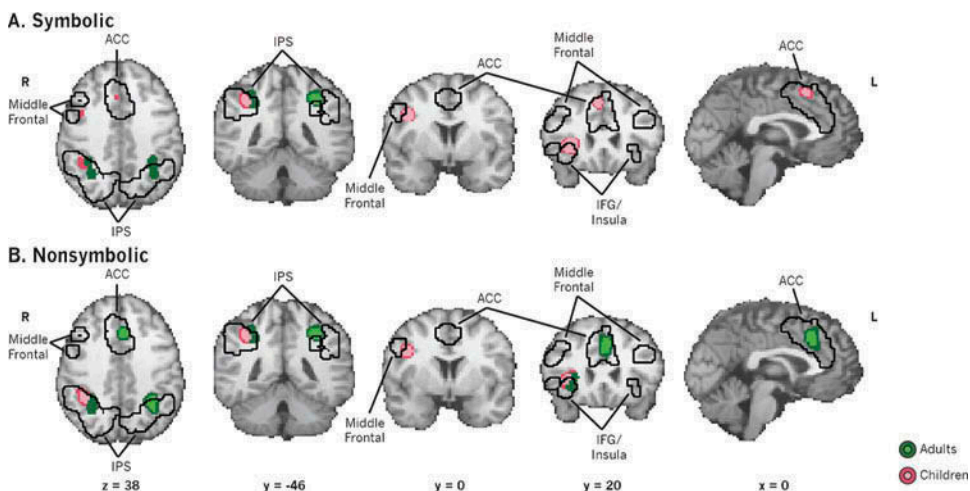

Figure 7. Meta-analytic summary of developmental neuroimaging studies. ALE results for adults (green) and children (pink) for symbolic (A) and nonsymbolic (B) numerical stimuli. ALE results were computed using GingerALE with an applied cluster threshold of $p < 0.05$ and are displayed on the 2 mm Colin brain in Talairach space downloaded from BrainMap (http://www.brainmap.org/ ale/). Brighter colors show clusters that survive cluster correction at a voxel-wise error rate of $p < 0.001$ and darker colors indicate clusters that survive cluster correction at a voxel-wise error rate of $p < 0.01$. For comparison, outlined areas represent ROIs from a symbolic to nonsymbolic numerical comparison task conducted with adults (Emerson & Cantlon, 2012; 2014; Number > Faces, Shapes, & Words). IPS = intraparietal sulcus, ACC = anterior cingulate cortex, IFG = inferior frontal gyrus.

of notation. Activation likelihood maps were calculated separately for children's symbolic number processing (101 foci from 11 articles; Figure 7A, pink), adults' symbolic number processing (27 foci from 6 articles; Figure 7A, green), children's nonsymbolic number (36 foci from 4 articles; Figure 7B, pink), and adults' nonsymbolic number (31 foci from 5 articles; Figure 7B, green).

As seen in Figure 7, children and adults engage common regions of the right IPS for symbolic and nonsymbolic processing and right IFG and insula for nonsymbolic processing, but show distinct patterns of recruitment in left IPS, DLPFC, and ACC. Children show unique recruitment of DLPFC across symbolic and nonsymbolic tasks. In contrast, adults show unique recruitment of left IPS (Table 2). This is in line with previous work that suggests that number processing in the right IPS matures earlier than the left IPS and that the development of the left IPS may be more related to the acquisition of symbolic number than the right IPS (Ansari & Dhital, 2006; Cantlon et al., 2006; Cantlon & Li, 2013; Emerson & Cantlon, 2014; Hyde et al., 2010; Rivera et al., 2005; Rosenberg-Lee, Barth, & Menon, 2011; Vogel et al., 2015).

For comparison, Figure 7 shows in black the outlines of regions activated by adults during a symbolic-to-nonsymbolic numerical matching task (Emerson & Cantlon, 2014; Numbers > Faces, Shapes, & Words, $p < 0.05$, corrected). In this task, subjects had to compare an Arabic numeral to an array of dots and press a button if they were the same value. The comparison shows that the patterns

Table 2. Talairach coordinates and maximum ALE values for regions of the brain consistently recruited during number processing across multiple studies.

Region	Hemisphere	Max ALE Value	TAL coordinates			Voxel-Wise Error Rate	Family-Wise Error Rate
			x	y	z		
Adults: Symbolic							
Parietal Cortex	Left	0.009	−30	−46	40	p < 0.01	p < 0.05
		0.008	−32	−56	36	p < 0.01	p < 0.05
		0.007	−32	−38	44	p < 0.01	p < 0.05
	Right	0.008	30	−56	36	p < 0.01	p < 0.05
		0.008	36	−56	26	p < 0.01	p < 0.05
		0.007	32	−44	40	p < 0.01	p < 0.05
Children: Symbolic							
Anterior Cingulate		0.013	4	10	48	p < 0.001	p < 0.05
		0.012	6	18	44	p < 0.001	p < 0.05
Insula	Right	0.019	34	18	4	p < 0.001	p < 0.05
		0.016	50	6	14	p < 0.01	p < 0.05
		0.008	40	12	16	p < 0.01	p < 0.05
Frontal Cortex	Right	0.024	40	2	32	p < 0.001	p < 0.05
Parietal Cortex	Right	0.016	38	−46	42	p < 0.01	p < 0.05
		0.009	30	−54	40	p < 0.01	p < 0.05
		0.007	40	−44	54	p < 0.01	p < 0.05
Adults: Nonsymbolic							
Anterior Cingulate		0.015	−2	18	38	p < 0.001	p < 0.05
		0.006	4	24	46	p < 0.01	p < 0.05
Insula	Right	0.008	30	22	6	p < 0.01	p < 0.05
		0.008	32	18	−2	p < 0.01	p < 0.05
Parietal Cortex	Left	0.014	−28	−48	42	p < 0.001	p < 0.05
		0.009	−32	−56	36	p < 0.001	p < 0.05
		0.008	−24	−60	48	p < 0.01	p < 0.05
	Right	0.009	30	−48	36	p < 0.01	p < 0.05
		0.009	30	−54	36	p < 0.01	p < 0.05
		0.008	36	−56	26	p < 0.01	p < 0.05
		0.006	32	−48	46	p < 0.01	p < 0.05
Children: Nonsymbolic							
Insula	Right	0.014	36	18	4	p < 0.001	p < 0.05
Frontal Cortex	Right	0.016	42	2	30	p < 0.001	p < 0.05
		0.009	50	8	22	p < 0.01	p < 0.05
		0.009	50	6	14	p < 0.01	p < 0.05
Parietal Cortex	Right	0.012	36	−46	38	p < 0.001	p < 0.05
		0.008	30	−54	40	p < 0.01	p < 0.05

of activation distilled from the meta-analysis largely overlap the mature, adult pattern of activation from a symbolic-to-nonsymbolic matching task. Across the studies in the meta-analysis, which largely only tested subjects on within-notation tasks (either symbolic or nonsymbolic, not both) children activated regions of DLPFC that adults did not (Figure 7, pink regions vs. green regions). In contrast, in the symbolic-to-nonsymbolic task shown in black outline, adults activated similar DLPFC regions to children. This suggests that regions of DLPFC that are recruited for symbolic-to-nonsymbolic matching tasks in adults are more likely to be recruited by children than adults during tasks that present a single numerical notation. A second important pattern, is that children display slightly greater recruitment of frontal regions for symbolic number than for nonsymbolic number. This suggests that the regions of the frontal cortex may be particularly important for symbolic number processing during childhood.

It is not the case, however, that adults do not recruit these DLPFC regions at all, nor is it the case that these regions are never involved in nonsymbolic numerical processing. For instance, we see engagement of right inferior frontal cortex for nonsymbolic number processing in adults. In addition, some studies have reported greater activation for adults than for children at these frontal loci (Ansari et al., 2005; Emerson & Cantlon, 2014; Haist, Wazny, Toomarian, & Adamo, 2015; Holloway & Ansari, 2010). Thus, the patterns presented in Figure 7 represent the common findings across studies, not the only findings. However, distilling across studies, adults are less likely than children to recruit DLPFC regions during numerical tasks.

As described above, one hypothesis for the function of frontal regions in numerical processing is the language-based integration of symbolic with nonsymbolic number representations (e.g., Cantlon et al., 2009; Nieder, 2009; Piazza et al., 2007). Inferior frontal and dorsolateral prefrontal cortex are thought to play a unique role in grounding symbolic number in approximate, nonverbal representations. For example, Nieder (2009) suggested that lateral prefrontal regions link neurons encoding the shapes of the numerical symbols in frontal cortex to the neurons encoding the nonsymbolic representations of quantity in the IPS. This hypothesis predicts limited recruitment of the prefrontal cortex for nonsymbolic number in cases where there is no reason to map nonsymbolic number to symbolic number. This hypothesis also predicts that children who have immature representations of symbolic numbers should show different degrees of engagement with frontal regions compared to adults. The data presented so far are consistent with these predictions.

A second possibility is that the role of frontal regions in numerical processing is domain-general cognitive control, and perhaps not specifically language-based. The hypothesis is that IFG and DLPFC activations reflect activities in the semantic and working memory circuits of frontal cortex (Ansari, 2008; Houdé, Rossi, Lubin, & Joliot, 2010; Lussier & Cantlon, 2016). Symbolic numerical representations require a level of semantic interpretation that is not required by the physical nonsymbolic representation of number—namely, a symbolic number has to be decoded from its arbitrary representation. As mentioned earlier, symbolic numbers are also unique compared to nonsymbolic representations because they have precise cardinal and ordinal representations in long-term memory and, unlike nonsymbolic quantities, are explicitly associated with other ordered semantic systems from human culture. Thus, symbolic numbers likely place unique demands on the engagement of semantic memory compared to nonsymbolic numbers. The patterns of frontal activation observed in numerical tasks are similar to patterns observed from the comparison of non-numerical semantic stimuli (Lussier & Cantlon, 2016) and are observed in studies of semantic memory that do not test numerical representation (e.g., Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Wagner, Paré-Blagoev, Clark, & Poldrack, 2001). The existing data summarized in Figure 7 are thus also consistent with the domain-general hypothesis that the IFG/insula, DLPFC, and ACC mediate the control of information in memory.

The IFG/insula and ACC may also play a more general role in numerical cognition even beyond semantic processing and working memory. Those regions show neural responses that are modulated by subjects' response times during comparisons of numerical and non-numerical stimuli (Emerson & Cantlon, 2012, 2014). Emerson and Cantlon (2012) found that activation levels in the IFG and
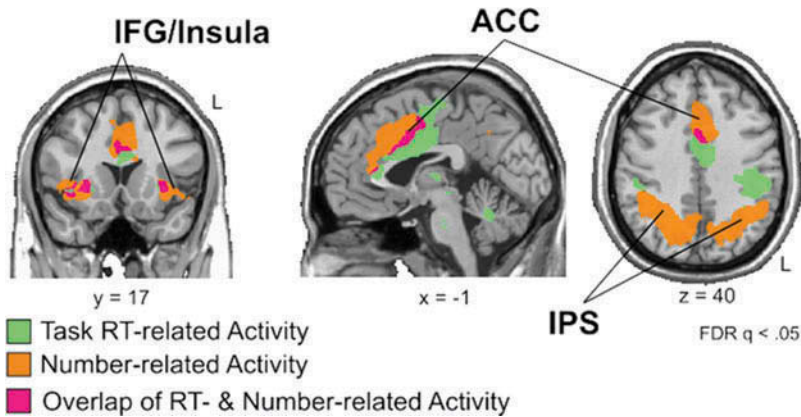
Figure 8. Regions that are modulated by trial response times (RT) in a matching task for faces, numbers, shapes, and words (RT+ as a parametric modulator), show greater amplitudes to number stimuli than control stimuli (Numbers > Faces, Shapes, and Words), and their overlap (FDR q < .05). Data are from (Emerson & Cantlon, 2012).

ACC were modulated by the duration of subjects' trial-by-trial RTs during face, number, word, and shape matching tasks (Figure 8). Longer RTs led to greater activation in those regions. RT is related both to the amount of cognitive effort required to resolve a trial, decision time, and the planning of the motor response. General task functions could account for the relation between RT and activation levels in the IFG/insula and ACC across tasks. Importantly, number-related activation in the IPS did not overlap task-general RT-related activation. Task-general RT-related activation in precentral and postcentral regions is likely related to motor planning and it is distinct from number-related IPS activation.

In summary, the IPS is recruited during numerical tasks across species, stages of human development, and whether the task is symbolic or nonsymbolic. Humans are unique from other animals in their capacity for symbolic numerical representation and there is some evidence from comparative fMRI studies that those unique features of human cognition are mediated by prefrontal regions. Humans are more likely than non-human primates to engage prefrontal regions during numerical and ordinal tasks. There are a number of attributes that distinguish the task of understanding symbolic numbers from the task of understanding nonsymbolic numbers including symbol decoding (language) and access to precise long-term memory representations (memory). The extent to which these unique operations are accomplished by frontal cortex in the service of numerical processing is an open question. Children's unique recruitment of frontal regions compared to adults' indicates that additional cognitive resources are needed to represent numerical stimuli in childhood compared to adulthood—the question is whether those extra resources are related to language, memory, or task execution.

Conclusion

Fundamental representational and logical abilities that promote human numerical reasoning have likely been in place for millions of years. The representation of number as an abstract property, the ability to order and perform arithmetic over those representations, and the ability to use sequential and iterative logic during quantitative judgments are primitive mechanisms in the sense that they are shared between human and non-human primates and develop early in human children. These primitive mechanisms are thought to be important for the development of symbolic number concepts in humans because they share important conceptual and structural properties with human counting and arithmetic. Some evidence indicates that children draw on primitive nonsymbolic representations during counting acquisition. The neural mechanisms that accomplish basic numerical functions in early childhood converge with

mechanisms children recruit during early-developing symbolic numerical operations. Human children must go beyond the primitive mechanisms to achieve a mature representation of symbolic numbers with rich semantic meanings. This requires uniquely human cognitive and neural mechanisms that can support interactions between the primitive mechanisms and human language and memory systems. At the neural level, regions of prefrontal cortex seem likely to serve these functions, but we currently lack a satisfying cognitive description of the computations carried out by those regions. Thus, current evidence indicates that children hijack some cognitive and neural functions from the evolutionarily primitive, analog numerical system to engage with systems of symbolic numerical thought during development—but the deeper nature of the interactions between the nonsymbolic and symbolic numerical systems in children's minds and brains remains unknown.

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