Numerosity

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Glossary

Nonsymbolic number Number of individuals in a set.
Numerosity Number of individuals in a set.
Representation (or mental representation) Pattern of brain activity or cognitive process that stands for an aspect of external reality.
Symbolic number Object or sign used to denote numerosity (e.g., one, 1).

Introduction

From counting change at the grocery store to finding a page in a book, numbers play a role in many facets of human life in modern societies. Symbolic numerical abilities also provide a powerful tool for scientific and technological advancement. In addition to its ubiquitous nature, numerosity presents an interesting challenge for the brain because it is not directly dependent on, or tied to, the particular features of individual items. For the brain to represent number, it must abstract away from basic sensory features of individuals to enumerate them. In this article, I will review current knowledge on the origins, development, and nature of numerosity in the brain.

Origins

Core Capacity for Numerosity

Although symbolic number and associated mathematical abilities are uniquely human, there is overwhelming evidence that the basic ability to mentally represent numerosity is present from birth and shared with a wide variety of nonhuman animals (Dehaene, 1996; Feigenson, Dehaene, & Spelke, 2004; Gallistel, 1990). Many studies have now shown numerical abilities in infancy (for a review, see Feigenson et al., 2004). For example, one study showed that neonates looked longer at a picture of objects that matched the number of tones they heard compared looking time toward a picture of a different number of items (Izard, Sann, Spelke, & Streri, 2009). Older infants are able to reliably detect changes in the number of items presented to them, even after controlling for other nonnumerical aspects such as the size, spacing, and position of items (e.g., Xu & Spelke, 2000). In visual habituation studies, for example, infants are repeatedly shown novel pictures containing the same number of objects until boredom (habituation images). Once bored, infants are then shown test pictures containing the same or a novel number of items. If the infant notices a difference in number, looking should increase to the test images containing a different number of items, but not to the test images containing the same number of items. Under these conditions, many studies have now shown that infants can detect changes in the number of items presented (see Feigenson et al., 2004 for a review). In all cases, however, infants' ability to discriminate or match numerosity is approximate or imprecise. Six- month-olds require a twofold difference in number before a numerical change can be detected (Xu & Spelke, 2000). The size of the numerical change necessary to detect a difference develops rapidly over the first year of life, with 3-month-olds requiring a threefold change to 9-month-olds requiring only a 1.5-fold change, suggesting an increase in precision of numerosity representation over the first year of life (Lipton & Spelke, 2003, 2004; Wood & Spelke, 2005; Xu & Arriaga, 2007). Similar findings have been observed using auditory tones or even actions of puppets, suggesting the underlying mental representation is not tied to a particular sensory system (Lipton & Spelke, 2003; Wood & Spelke, 2005). This core ability to represent the approximate numerosity of sets without counting, formal instruction, or even spoken language has been referred to as the approximate number system (ANS) or 'number sense' (see Dehaene, 1997; Feigenson et al., 2004).

The functional brain response of infants to numerosity mirrors the behavioral limits of the ANS (Hyde & Spelke, 2011; Libertus, Pruitt, Woldorff, & Brannon, 2009). Event-related brain potentials (ERPs) in 5–6-month-old infants, for example, show that changes in the number of items displayed on a screen elicit a posterior parietal brain response proportional to the numerical ratio of change between the numbers in the same way that behavioral performance has been shown to be influenced by the numerical ratio between numbers (Hyde & Spelke, 2011, or see Libertus et al., 2009 for EEG evidence). A combination of source estimation techniques, ERPs, and optical imaging suggests that processing of number arises largely from the right parietal brain regions in infants (Hyde, Boas, Blair, & Carey, 2010; Izard, Dehaene-Lambertz, & Dehaene, 2008) (see **Figure 1**). Even within the first year, this region appears to be specialized for numerosity, as it does not respond to changes in the size, spacing, features, or shape of the individual objects (Hyde & Spelke, 2011; Hyde et al., 2010; Izard et al., 2008).

Development

Unilateral to Bilateral Parietal Shift

As infants develop into children, they begin to acquire and attribute meaning to symbolic systems of number such as number words and digits. Starting as early as 2 years, children

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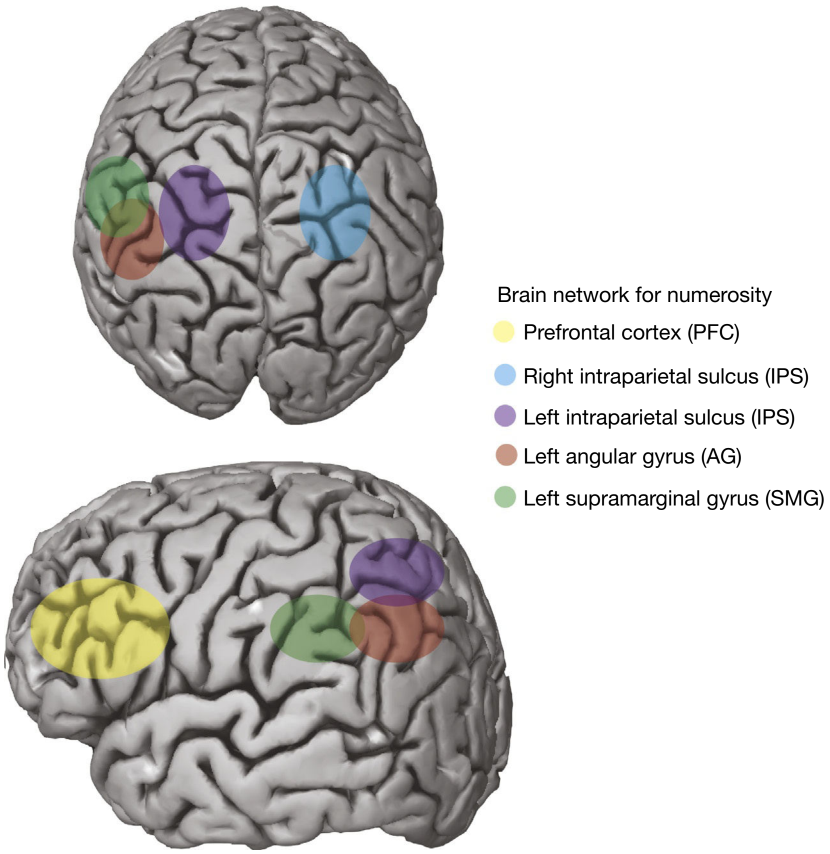

Figure 1 Brain regions associated with numerosity.

are able to recite the number words or count list (Wynn, 1990, 1992). Within the next 1.5–2 years, they come to understand what the number words mean and how to use to them to count (Le Corre & Carey, 2007; Le Corre, Van de Walle, Brannon, & Carey, 2006). During this same time, what was initially a right-lateralized brain response to numerosity becomes more bilateral. For example, Cantlon, Brannon, Carter, and Pelphrey (2006) showed regions selective for numerosity were largely restricted to right parietal regions in the intraparietal sulcus (IPS) and superior parietal lobule in 4-year-olds, while adults showed numerosity-selective regions in both hemispheres.

Over development, symbolic numbers become linked to the ANS. Although the temporal relationship of this mapping between systems and its role for learning is debated (see Piazza, 2010 for a review), it is clear that during or shortly after counting develops, the two systems become associated and this association persists throughout the life span. As a result, the same regions that respond to nonsymbolic numerosity also begin to respond to symbolic numbers (Holloway & Ansari, 2010; Temple & Posner, 1998). The association between symbolic and nonsymbolic numbers also results in a behavioral influence of approximate numerosity on exact, symbolic number tasks (Moyer & Landauer, 1967; Reynvoet, De Smedt, & Van den Bussche, 2009; Temple & Posner, 1998). For example, a distance effect arises, where the speed and accuracy to compare two symbolic numbers (i.e., say which is larger) are a function of the numerical distance between them in the same way behavioral performance on comparisons of sets of objects is a function of the numerical distance between them (e.g., Moyer & Landauer, 1967). A distance effect is also present in the brain response to symbolic number tasks as well (e.g., Dehaene, 1997; Temple & Posner, 1998). For example, Temple and Posner (1998) showed that comparing two digits or two nonsymbolic arrays elicited modulation of the same posterior parietal ERP response in children and adults. The distance effect is substantially diminished in children with developmental dyscalculia, a learning disability specific to mathematics (e.g., Price, Holloway, Rasanen, Vesterinen, & Ansari, 2007), suggesting a functional relationship between behavioral performance and the cortical distance effect.

Some evidence suggests that the link between the ANS and symbolic numbers is more than a simple association (see Halberda, Mazzocco, & Feigenson, 2008). In fact, it has been hypothesized that the ANS forms the basis on which symbolic number systems develop (see Piazza, 2010 for a review). In support of this view, individual differences in approximate number precision predict mathematics achievement scores in young children, older children, college students, and adults (e.g., Gilmore, McCarthy, & Spelke, 2010; Halberda et al., 2008; Starr, Libertus, & Brannon, 2013). Furthermore, training or practice with approximate number tasks improves exact, symbolic mathematics performance (Hyde, Khanum, & Spelke, 2014; Park & Brannon, 2013).

Left Parietal Involvement in Number

Involvement of the left parietal regions in number processing, including the left IPS, left supramarginal gyrus (SMG), and left angular gyrus (AG), increases over later childhood (e.g., Ansari, Garcia, Lucas, Hamon, & Dhital, 2005; Cantlon & Li, 2013; Cantlon et al., 2006; Rivera, Reiss, Eckert, & Menon, 2005) (see **Figure 1**). Using an innovative approach to index neural maturity (based on the adult functional brain response as the standard), Cantlon and Li (2013) showed that the functional maturity of the left IPS in 4–10-year-old children, previously identified as sensitive to number, predicted formal mathematics performance. Another study showed that left parietal involvement continues to increase for symbolic numbers and mathematical processing from 8–19 years of age, a time when even more advanced mathematics is acquired (Rivera et al., 2005). By adulthood, bilateral regions of the IPS respond to the numerosity (Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004; Piazza, Pinel, Le Bihan, & Dehaene, 2007) and damage to these regions selectively impairs the ability to think about number (see Dehaene, Piazza, Pinel, & Cohen, 2003 for a review). The cause of the shift from a unilateral right parietal response to number early in development to a bilateral response is not known. However, most hypothesize that the acquisition and refinement of a symbolic number system and the associated linguistic symbols contribute to this developmental shift (see Ansari, 2008 for a review). The increased involvement of the left SMG and AG, areas known to be involved in linking symbols to their meaning more generally, supports this view (see Dehaene et al., 2003, for a review).

Prefrontal Cortical Involvement in Number

Involvement of the prefrontal cortex (PFC) in numerosity processing also appears to change over development. Specifically, involvement of PFC decreases over development (Ansari & Dhital, 2006; Ansari et al., 2005; Cantlon et al., 2006, 2009; Rivera et al., 2005) (see **Figure 1**). One idea is that processing of number simply becomes more efficient, moving from a more effortful to a more automatic process (see Ansari, 2008). Studies of dyscalculia show that children that struggle with mathematics also show more PFC activation to number-related tasks (Ansari et al., 2005). Decreases in activity in the anterior cingulate cortex associated with attention and the hippocampus associated with memory have also been observed over development (Rivera et al., 2005), further supporting the view of an increase in automaticity.

PFC itself is thought to play a role in the mapping between number symbols and the numbers they represent. Children in the midst of learning and strengthening these associations show more activity than adults who have already established strong links. A recent fMRI training study in adults showed that activity in both the left parietal and the prefrontal regions was associated with learning to map a new symbol system onto quantities (Lyons & Ansari, 2009). However, only left IPS activity was related to learning proficiency, suggesting PFC may play a supportive role, rather than a direct role, in the numerosity–symbol mapping process.

The Role of White Matter Structures and Connections

Emerging evidence suggests that white matter structure and connections between cortical regions are important to numerical abilities (Emerson & Cantlon, 2012; Matejko, Price, Mazzocco, & Ansari, 2013). Specifically, emerging evidence shows that the strength of connections between number-responsive PFC and IPS is related numerical abilities (Emerson & Cantlon, 2012). Furthermore, integrity (fractional isotropy) of white matter microstructure in left parietal regions correlates with scores on mathematics achievement tests after controlling for general cognitive ability and age (Matejko et al., 2013). Current knowledge in this area, however, is rather limited, but likely to increase with advances in technology and analysis techniques to measure white matter structure and connectivity in the brain.

Nature of Number Representation

Specialization

There remains some debate as to whether number-sensitive cortical regions are also responsive to other nonnumerical magnitudes or whether those regions are specialized for number (e.g., Shuman & Kanwisher, 2004; Walsh, 2003; Piazza et al., 2004; Hyde et al., 2010). The inherent problem in testing for specialization, or domain specificity, in the brain is that it is impossible to test a given domain against every other possible domain. Some posit a generalized magnitude system that is sensitive to spatial, temporal, and numerical magnitudes (e.g., Walsh, 2003). The idea of a generalized magnitude system garnered support from parietal lesion patients who often suffered with deficits in at least two of the three proposed magnitude domains, as well as behavioral evidence showing interactions of each domain on the perception or performance in the other (see Walsh, 2003 for a review). Some neuroimaging studies provide evidence for numerical domain specificity in the IPS (e.g., Hyde et al., 2010; Piazza et al., 2004), while others provide evidence against it (e.g., Shuman & Kanwisher, 2004). The current evidence, however, suggests a patchwork where at least some subregions of the IPS may be selective for number, while other subregions also respond to other nonnumerical magnitudes (see Cohen Kadosh et al., 2005; Pinel, Piazza, Le Bihan, & Dehaene, 2004). For example, Pinel and colleagues (2004) found areas within the IPS that responded to both numerical magnitude and physical magnitude (i.e., size), other areas that responded to numerical magnitude only, and no areas that responded to both brightness and number. This work suggests that while generalized magnitude representations are likely present, some regions of the parietal lobe are also specialized for number.

Abstraction

Numerical information can be received in a variety of formats and senses. We can see a certain number of objects, hear a certain number of tones, or feel a certain number of taps. We can read an Arabic digit, hear someone say a number, or read a written word. While numerical information has to be extracted from the sense or format in which it is received, one question that arises is whether numerosity representation in the brain is completely format-dependent or whether, at some level in the brain, it is abstracted way from the sense and format.

Brain research and behavioral work provides evidence that number is abstracted away from the format of presentation. For example, individuals show similar behavioral abilities to make number comparisons in different formats (e.g., digits, words, and nonsymbolic objects) and senses (e.g., auditory tones and visual displays), suggesting a common abstract representation of number (e.g., Barth, Kanwisher, & Spelke, 2003; Pinel, Dehaene, Riviere, & LeBihan, 2001). Furthermore, many studies show that overlapping regions of the IPS are active when processing numbers in a variety of symbolic and nonsymbolic forms (e.g., Cantlon et al., 2009; Eger, Sterzer, Russ, Giraud, & Kleinschmidt, 2003; Fias, Lammertyn, Reynvoet, Dupont, & Orban, 2003; Pinel et al., 2001; Venkatraman, Ansari, & Chee, 2005). Others show a similar neural distance effect regardless of format (Libertus, Woldorff, & Brannon, 2007). The strongest evidence to date, however, comes from a functional neuroimaging study showing that after being repeatedly shown, or adapted to, novel pictures of the same number of objects, IPS activity rebounds to a novel picture of a different number of objects or an Arabic digit of a different number, but not to a novel picture of the same number of items or an Arabic digit of the same number (Piazza et al., 2007). Critics argue that conjunctions in activity between formats may arise as a result of task demands or a lack of imaging resolution (see Cohen Kadosh & Walsh, 2009) and under other conditions, evidence of format dependence in number-sensitive IPS regions has been provided (Cohen Kadosh et al., 2011). As such, further work is needed before a consensus can be reached regarding numerical abstraction in the brain.

Neural Coding of Number

A final open question is how numerosity is actually physically instantiated by firing patterns of cells. Neural network models suggest at least two ways this may happen. Some propose an accumulator, where sequential impulses encode individual items and numerosity is derived from the total magnitude resulting from the accumulation process (e.g., Meck & Church, 1983; Zorzi & Butterworth, 1999). Others posit a type of numerosity detector, where units are identified in parallel and then integrated to yield an estimate of the particular number of items present (e.g., Dehaene & Changeux, 1993; Verguts & Fias, 2004). Both types of mechanisms have been shown to account behavioral effects in numerical processing (Dehaene & Changeux, 1993; Meck & Church, 1983; Verguts & Fias, 2004; Zorzi & Butterworth, 1999).

Recordings from single neurons in nonhuman primates also provide evidence for both these mechanisms (see Nieder & Dehaene, 2009). Neurons in the lateral intraparietal area of the macaque, for example, have been shown to respond monotonically to either increasing or decreasing number (Roitman, Brannon, & Platt, 2007). On the other hand, others have shown that single neurons within the lateral prefrontal cortex and ventral intraparietal area of the macaque are selectively tuned to particular numerical values and their response is independent of other nonnumerical features of individual items (Nieder, Freedman, & Miller, 2002; Nieder & Miller, 2004; or see Nieder & Dehaene, 2009, for a review). Activity in these neurons is related to behavioral performance of the animals on number comparison or matching tasks (e.g., Nieder & Merten, 2007; Nieder & Miller, 2004; Nieder et al., 2002). Furthermore, the temporal pattern of firing, in addition to the rate or magnitude of firing, has also been shown to carry information regarding numerosity (Tudusciuc & Nieder, 2007). Commonalities in the anatomical region, the function brain response, and the link between the response and behavior in nonhuman primates and humans suggest that such coding could feasibly reside in the human brain as well (see Nieder & Dehaene, 2009, for a review).

The resolution of current noninvasive human neuroimaging methods is too course to reliably determine how individual human brain cells code numerical information. However, recent advances in multivoxel pattern classification algorithms have yielded some interesting findings about how information might be coded across (voxels or subregions) a region rather than in the average response of that region. Specifically, one recent study showed that investigators could reliability determine how many dots participants viewed by decoding the pattern of activation across voxels in IPS (Eger et al., 2009). Future work using pattern classification techniques and increases in the resolution of noninvasive imaging will undoubtedly shed further light on how number is coded in human brain.

Conclusion

Overwhelming evidence suggests that evolution provided us with the capacity to mentally represent approximate numerosity (Dehaene, 1997; Feigenson et al., 2004; Gallistel, 1990). This ability appears to arise, in part, from a number-selective region of the right IPS (e.g., Hyde et al., 2010; Izard et al., 2008). Experience, language, and number-specific knowledge acquisition are associated with increased involvement of left parietal structures including the left IPS, SMG, and AG (Cantlon et al., 2006; Rivera et al., 2005). Current evidence suggests that what results is a bilateral parietal brain system that represents both symbolic and nonsymbolic numbers (Cantlon et al., 2009; Fias et al., 2003; Pinel et al., 2001)(see **Figure 1**). At some level, this system may even respond to number in a sense- and format-independent manner (Eger et al., 2003; Piazza et al., 2007). As such, the brain accomplishes the impressive feat of abstracting away from basic sensory features of individuals to represent numerosity and further links particular numerosities with particular cultural and/or linguistic symbols.

See also: **INTRODUCTION TO ANATOMY AND PHYSIOLOGY**: Development of Structural and Functional Connectivity; Lateral and Dorsomedial Prefrontal Cortex and the Control of Cognition; Posterior Parietal Cortex: Structural and Functional Diversity.

References

Ansari, D. (2008). Effects of development and enculturation on number representation in the brain. *Nature Reviews. Neuroscience*, *9*(4), 278–291.
Ansari, D., & Dhital, B. (2006). Age-related changes in the activation of the intraparietal sulcus during nonsymbolic magnitude processing: An event-related functional magnetic resonance imaging study. *Journal of Cognitive Neuroscience*, *18*(11), 1820–1828.

Ansari, D., Garcia, N., Lucas, E., Hamon, K., & Dhital, B. (2005). Neural correlates of symbolic number processing in children and adults. *NeuroReport*, *16*(16), 1769–1773.

Barth, H., Kanwisher, N., & Spelke, E. (2003). The construction of large number representations in adults. *Cognition*, *86*(3), 201–221.

Cantlon, J. F., Brannon, E. M., Carter, E. J., & Pelphrey, K. A. (2006). Functional imaging of numerical processing in adults and 4-y-old children. *PLoS Biology*, *4*(5), e125.

Cantlon, J. F., & Li, R. (2013). Neural activity during natural viewing of Sesame Street statistically predicts test scores in early childhood. *PLoS Biology*, *11*(1), e1001462.

Cantlon, J. F., Libertus, M. E., Pinel, P., Dehaene, S., Brannon, E. M., & Pelphrey, K. A. (2009). The neural development of an abstract concept of number. *Journal of Cognitive Neuroscience*, *21*(11), 2217–2229.

Cohen Kadosh, R., Bahrami, B., Walsh, V., Butterworth, B., Popescu, T., & Price, C. J. (2011). Specialization in the human brain: The case of numbers. *Frontiers in Human Neuroscience*, *5*(62), 1–9.

Cohen Kadosh, R., Henik, A., Rubinsten, O., Mohr, H., Dori, H., van de Ven, V., et al. (2005). Are numbers special? The comparison systems of the human brain investigated by fMRI. *Neuropsychologia*, *43*(9), 1238–1248.

Cohen Kadosh, R., & Walsh, V. (2009). Numerical representation in the parietal lobes: Abstract or not abstract? *Behavioral and Brain Sciences*, *32*(3–4), 313–328.

Dehaene, S. (1996). The organization of brain activations in number comparison: Event-related potentials and the additive-factors method. *Journal of Cognitive Neuroscience*, *8*(1), 47–68.

Dehaene, S. (1997). *The number sense*. New York: Oxford University Press.

Dehaene, S., & Changeux, J. P. (1993). Development of elementary numerical abilities: A neuronal model. *Journal of Cognitive Neuroscience*, *5*(4), 390–407.

Dehaene, S., Piazza, M., Pinel, P., & Cohen, L. (2003). Three parietal circuits for number processing. *Cognitive Neuropsychology*, *20*(3–6), 487–506.

Eger, E., Michel, V., Thirion, B., Amadon, A., Dehaene, S., & Kleinschmidt, A. (2009). Deciphering cortical number coding from human brain activity patterns. *Current Biology*, *19*(19), 1608–1615.

Eger, E., Sterzer, P., Russ, M. O., Giraud, A. L., & Kleinschmidt, A. (2003). A supramodal number representation in human intraparietal cortex. *Neuron*, *37*(4), 719–726.

Emerson, R. W., & Cantlon, J. F. (2012). Early math achievement and functional connectivity in the fronto-parietal network. *Developmental Cognitive Neuroscience*, *2*, S139–S151.

Feigenson, L., Dehaene, S., & Spelke, E. S. (2004). Core systems of number. *Trends in Cognitive Sciences*, *8*(7), 307–314.

Fias, W., Lammertyn, J., Reynvoet, B., Dupont, P., & Orban, G. A. (2003). Parietal representation of symbolic and nonsymbolic magnitude. *Journal of Cognitive Neuroscience*, *15*(1), 47–56.

Gallistel, C. R. (1990). *The organization of learning*. Cambridge, MA: Bradford Books.

Gilmore, C. K., McCarthy, S. E., & Spelke, E. S. (2010). Non-symbolic arithmetic abilities and mathematics achievement in the first year of formal schooling. *Cognition*, *115*(3), 394–406.

Halberda, J., Mazzocco, M. M.M, & Feigenson, L. (2008). Individual differences in non-verbal number acuity correlate with maths achievement. *Nature*, *455*(7213), 665–669.

Holloway, I. D., & Ansari, D. (2010). Developmental specialization in the right intraparietal sulcus for the abstract representation of numerical magnitude. *Journal of Cognitive Neuroscience*, *22*(11), 2627–2637.

Hyde, D. C., Boas, D. A., Blair, C., & Carey, S. (2010). Near-infrared spectroscopy shows right parietal specialization for number in pre-verbal infants. *NeuroImage*, *53*(2), 647–652.

Hyde, D. C., Khanum, S., & Spelke, E. S. (2014). Brief non-symbolic, approximate number practice enhances subsequent exact symbolic arithmetic in children. *Cognition*, *131*(1), 92–107.

Hyde, D. C., & Spelke, E. S. (2011). Neural signatures of number processing in human infants: Evidence for two core systems underlying numerical cognition. *Developmental Science*, *14*(2), 360–371.

Izard, V., Dehaene-Lambertz, G., & Dehaene, S. (2008). Distinct cerebral pathways for object identity and number in human infants. *PLoS Biology*, *6*(2), e11.

Izard, V., Sann, C., Spelke, E. S., & Streri, A. (2009). Newborn infants perceive abstract numbers. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(25), 10382–10385.

Le Corre, M., & Carey, S. (2007). One, two, three, four, nothing more: An investigation of the conceptual sources of the verbal counting principles. *Cognition*, *105*(2), 395–438.

Le Corre, M., Van de Walle, G., Brannon, E. M., & Carey, S. (2006). Re-visiting the competence/performance debate in the acquisition of the counting principles. *Cognitive Psychology*, *52*(2), 130–169.

Libertus, M. E., Pruitt, L. B., Woldorff, M. G., & Brannon, E. M. (2009). Induced alpha-band oscillations reflect ratio-dependent number discrimination in the infant brain. *Journal of Cognitive Neuroscience*, *21*(12), 2398–2406.

Libertus, M. E., Woldorff, M. G., & Brannon, E. M. (2007). Electrophysiological evidence for notation independence in numerical processing. *Behavioral and Brain Functions*, *3*(1), 1–15.

Lipton, J. S., & Spelke, E. S. (2003). Origins of number sense: Large number discrimination in human infants. *Psychological Science*, *14*(5), 396–401.

Lipton, J. S., & Spelke, E. S. (2004). Discrimination of large and small numerosities by human infants. *Infancy*, *5*(3), 271–290.

Lyons, I. M., & Ansari, D. (2009). The cerebral basis of mapping nonsymbolic numerical quantities onto abstract symbols: An fMRI training study. *Journal of Cognitive Neuroscience*, *21*(9), 1720–1735.

Matejko, A. A., Price, G. R., Mazzocco, M. M., & Ansari, D. (2013). Individual differences in left parietal white matter predict math scores on the Preliminary Scholastic Aptitude test. *NeuroImage*, *66*, 604–610.

Meck, W. H., & Church, R. M. (1983). A mode control model of counting and timing processes. *Journal of Experimental Psychology: Animal Behavior Processes*, *9*(3), 320.

Moyer, R. S., & Landauer, T. K. (1967). Time required for judgments of numerical inequality. *Nature*, *215*, 1519–1520.

Nieder, A., & Dehaene, S. (2009). Representation of number in the brain. *Annual Review of Neuroscience*, *32*, 185–208.

Nieder, A., Freedman, D. J., & Miller, E. K. (2002). Representation of the quantity of visual items in the primate prefrontal cortex. *Science*, *297*(5587), 1708–1711.

Nieder, A., & Merten, K. (2007). A labeled-line code for small and large numerosities in the monkey prefrontal cortex. *The Journal of Neuroscience*, *27*(22), 5986–5993.

Nieder, A., & Miller, E. K. (2004). A parieto-frontal network for visual numerical information in the monkey. *Proceedings of the National Academy of Sciences of the United States of America*, *101*(19), 7457–7462.

Park, J., & Brannon, E. M. (2013). Training the approximate number system improves math proficiency. *Psychological Science*, *24*(10), 2013–2019.

Piazza, M. (2010). Neurocognitive start-up tools for symbolic number representations. *Trends in Cognitive Sciences*, *14*(12), 542–551.

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.

Piazza, M., Pinel, P., Le Bihan, D., & Dehaene, S. (2007). A magnitude code common to numerosities and number symbols in human intraparietal cortex. *Neuron*, *53*(2), 293–305.

Pinel, P., Dehaene, S., Riviere, D., & LeBihan, D. (2001). Modulation of parietal activation by semantic distance in a number comparison task. *NeuroImage*, *14*(5), 1013–1026.

Pinel, P., Piazza, M., Le Bihan, D., & Dehaene, S. (2004). Distributed and overlapping cerebral representations of number, size, and luminance during comparative judgments. *Neuron*, *41*(6), 983–993.

Price, G. R., Holloway, I., Rasanen, P., Vesterinen, M., & Ansari, D. (2007). Impaired parietal magnitude processing in developmental dyscalculia. *Current Biology*, *17*(24), R1042–R1043.

Reynvoet, B., De Smedt, B., & Van den Bussche, E. (2009). Children's representation of symbolic magnitude: The development of the priming distance effect. *Journal of Experimental Child Psychology*, *103*(4), 480–489.

Rivera, S. M., Reiss, A. L., Eckert, M. A., & Menon, V. (2005). Developmental changes in mental arithmetic: Evidence for increased functional specialization in the left inferior parietal cortex. *Cerebral Cortex*, *15*(11), 1779–1790.

Roitman, J. D., Brannon, E. M., & Platt, M. L. (2007). Monotonic coding of numerosity in macaque lateral intraparietal area. *PLoS Biology*, *5*(8), e208.

Shuman, M., & Kanwisher, N. (2004). Numerical magnitude in the human parietal lobe: Tests of representational generality and domain specificity. *Neuron*, *44*(3), 557–569.

Starr, A., Libertus, M. E., & Brannon, E. M. (2013). Number sense in infancy predicts mathematical abilities in childhood. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(45), 18116–18120.

Temple, E., & Posner, M. (1998). Brain mechanisms of quantity are similar in 5-year-old children and adults. *Proceedings of the National Academy of Sciences of the United States of America*, *95*(13), 7836–7841.

Tudusciuc, O., & Nieder, A. (2007). Neuronal population coding of continuous and discrete quantity in the primate posterior parietal cortex. *Proceedings of the National Academy of Sciences*, *104*(36), 14513–14518.

Venkatraman, V., Ansari, D., & Chee, M. W. (2005). Neural correlates of symbolic and non-symbolic arithmetic. *Neuropsychologia*, *43*(5), 744–753.

Verguts, T., & Fias, W. (2004). Representation of number in animals and humans: A neural model. *Journal of Cognitive Neuroscience*, *16*(9), 1493–1504.

Walsh, V. (2003). A theory of magnitude: Common cortical metrics of time, space and quantity. *Trends in Cognitive Sciences*, *7*(11), 483–488.

Wood, J. N., & Spelke, E. S. (2005). Infants' enumeration of actions: Numerical discrimination and its signature limits. *Developmental Science*, *8*(2), 173–181.

Wynn, K. (1990). Children's understanding of counting. *Cognition*, *36*(2), 155–193.

Wynn, K. (1992). Addition and subtraction by human infants. *Nature*, *358*(6389), 749–750.

Xu, F., & Arriaga, R. I. (2007). Number discrimination in 10-month-old infants. *British Journal of Developmental Psychology*, *25*(1), 103–108.

Xu, F., & Spelke, E. S. (2000). Large number discrimination in 6-month old infants. *Cognition*, *74*(1), B1–B11.

Zorzi, M., & Butterworth, B. (1999). A computational model of number comparison. In M. Hahn, & S. C. Stoness (Eds.), *Proceedings of the twenty first annual conference of the cognitive science society* (pp. 778–783). Mahwah, NJ: Erlbaum.