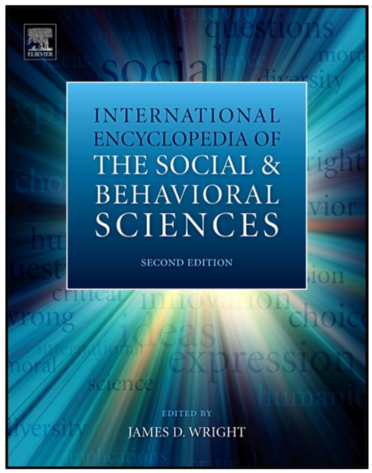

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Numbers and Number Sense

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Abstract

This article reviews several canonical signatures of number processing and the proposed theoretical interpretations of these signatures. It examines the biological origins of number sense in humans and nonhuman species alike, how to conceptualize the notion of numbers without symbolic form, and the role that number sense may play in human development. Symbolic numbers are discussed in terms of their history and the leading ideas about how the human brain assigns meaning to these crucial building blocks of modern human society.

Introduction

It is difficult to think of an aspect of modern society that has not been fundamentally shaped by the application of mathematics. Numbers, it may be argued, provide the basic cognitive scaffolding around which mathematical thinking is eventually constructed. The study of how numbers are represented and manipulated at both cognitive and neural levels thus provides a window into how the brain acquires and hones perhaps one of its most effective tools for shaping the world around us: mathematics. At the broadest level, the study of numerical cognition has divided numbers into two categories: symbolic and nonsymbolic. Symbolic numbers typically refer to exact quantities and are typically studied in written (e.g., Indo-Arabic numerals) or spoken (number words) form. Nonsymbolic magnitudes tend to be more approximate in nature – for instance, one may rapidly estimate which of two groups of dots contains more objects without counting or explicit reference to a symbolic numerical label. Number processing in both forms – symbolic and nonsymbolic – has been extensively studied in human children and adults, as well as many different nonhuman species. Methodological approaches tend to be behavioral (e.g., response times and/or error rates in numerical judgments) or neural (e.g., noninvasive neuroimaging in humans, as well as single-cell recording in nonhuman primates).

In the sections that follow, I review several canonical signatures of number processing and the proposed theoretical interpretations of these signatures. I then examine the biological origins of number sense in humans and nonhuman species alike, how to conceptualize the notion of numbers without symbolic form, and the role that number sense may play in human development. Finally, I discuss symbolic numbers in terms of their history and the leading ideas about how the human brain assigns meaning to these crucial building blocks of modern human society.

Signatures of Number Processing

There are several behavioral and neural signatures of number processing commonly found and discussed throughout the field of numerical cognition. Interpreting these effects has helped shape the ongoing debate about how numbers are represented and processed in the brain.

Numerical Distance Effect

Perhaps the most commonly cited numerical signature is the numerical distance effect. Note that the term 'distance' is something of a misnomer here, as it refers strictly to the absolute numerical difference between numbers, and not the physical distance between them. When an individual is asked to decide which of two numbers is numerically greater (commonly referred to as a numerical comparison task), performance depends systematically on the numerical difference between the two numbers. Performance tends to be worse (longer response times and higher error rates) when the numbers being compared are numerically close (e.g., performance on 5 vs 6 is worse than on 3 vs 8). This effect has been shown in both adults (Moyer and Landauer, 1967; Buckley and Gillman, 1974) and children (Sekuler and Mierkiewicz, 1977; Rubinsten et al., 2002). Moreover, neuroimaging studies have shown that brain responses – particularly in the intraparietal sulcus (IPS) – are modulated specifically by numerical distance during numerical comparison tasks (Pinel et al., 2001; Kaufmann et al., 2005; Ansari et al., 2006; Mussolin et al., 2013).

A related effect uses priming instead of comparison as a means of measuring the influence of numerical distance on brain and behavioral responses. In a priming paradigm, participants see a very brief stimulus (called a prime) immediately prior to completing some simple task. For example, when asked to name a number, numerically close primes lead to more facilitation (faster response times) than do numerically distant primes (Reynvoet et al., 2002). This effect is found in children as young as first grade, and is similar to that seen in adults (Reynvoet et al., 2009). The numerical distance between prime and target numbers also modulates neural responses in parietal cortex (Notebaert et al., 2010). In sum, numerical distance effects are present in both adults and children, influence both behavioral and neural responses, and are detectable whether measured via comparison or priming.

Numerical Ratio Effect

Another numerical signature is the numerical ratio effect, which refers to the ratio between two numbers, $\left(\frac{n_1}{n_2}\right)$, typically where $n_1 < n_2$. (Notice that the ratio effect differs from the distance effect primarily in that the former takes into account the numerical size of the numbers in question. For example the distances between the pairs (2, 3) and (8, 9) are both 1;

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however, they differ in ratio $\left(\frac{2}{3}\neq\frac{8}{9}\right)$.) In number comparison tasks (subjects decide which of the two numbers is numerically greater), performance tends to be worse as ratio approaches 1 (e.g., Lyons and Beilock, 2009). Six-month-old infants' looking times are influenced by numerical ratio. For example, if an infant sees 16 items repeatedly displayed on a screen, the infant will look longer at the screen when it changes to 32 items (ratio = 0.5). However, the child will not increase its looking time when the screen changes from 16 to 24 items (ratio = 0.67) (Xu et al., 2005). The ratio at which children can distinguish between such perceptual magnitudes becomes more precise (i.e., closer to 1) as children get older (Halberda and Feigenson, 2008), asymptoting at around $\frac{10}{11}$ in adults (Halberda and Feigenson, 2008; Pica et al., 2004).

The method most commonly used for assessing neural responses as a function of numerical ratio is called adaptation. An individual whose brain is being imaged will passively view several repetitions of a given number (e.g., 6). This passive repetition is associated with a steady reduction in the neural response to the repeated (standard) number; that is, the relevant brain regions are thus 'adapted' (i.e., habituated) to the repeated stimulus (Grill-Spector et al., 2006). Researchers will then intermittently present different (deviant) numbers (e.g., one of 4, 5, 7, 8, etc.) and measure the resulting neural response. One can then plot the brain responses to the deviant numbers as a function of their numerical ratio relative to the standard number. Neural responses in the parietal lobe (especially the IPS) tend to be systematically greater as the ratio between the standard and the deviant diverges from 1 (Piazza et al., 2004; Holloway et al., 2013).

A close derivative of numerical ratio is sometimes referred to as the numerical Weber fraction, or w, which has become an especially popular measure of numerical comparison performance (e.g., Halberda et al., 2008, 2012). One reason for this is that w is an especially strong predictor of how accurately individuals compare perceptual magnitudes (such as arrays of dots). When fitting sample means, the R^2 fit between estimated w and actual error rates is often upward of 0.9 for children, monkeys, and adults (Pica et al., 2004; Cantlon and Brannon, 2007; Halberda and Feigenson, 2008; Lyons and Beilock, 2011).

A few points of caution with respect to w are worth noting, however. First, w is very closely related to numerical ratio. This is because the formula for estimating w when comparing two numbers n_1 and n_2 ($n_1 < n_2$) relies on the value $k = \frac{n_2 - n_1}{\sqrt{2(n_2^2 + n_1^2)}}$, which is very highly correlated with the simple ratio between n_1 and $n_2 \left(\frac{n_1}{n_2}\right)$ (for full details on the formula for estimating w, see Pica et al., 2004). For example, in a stimulus set containing all possible (nonequal) number pairs from the range 1–10, k and $\frac{n_1}{n_2}$ will be correlated at $r = -0.999$. Thus, an estimate of w should be nearly identical to a ratio effect. Second, w can only be assessed with respect to error rates and not response times. This may be especially problematic when examining symbolic number comparisons (i.e., using Indo-Arabic numerals) in adults, where error rates may be very close to zero, and hence the majority of meaningful performance variability is often found in response times. Finally, Inglis and Gilmore (2014) recently showed that test/retest reliability for both w and ratio effects is poor (though see also Price et al., 2012; for issues regarding reliability of symbolic distance effects, see Maloney et al., 2010). On the other hand, Inglis and Gilmore (2014) showed that reliability for overall average accuracy was quite high; hence, if one is concerned with individual differences (e.g., relating numerical performance with other measures, such as math achievement or IQ), then one may be better off forgoing measures related to numerical distance or ratio altogether.

In sum, like numerical distance, the influence of numerical ratio on both brain and behavioral responses has been identified across a wide range of ages, measures, and experimental paradigms. There has been strong recent interest in using w – a close cousin of numerical ratio. While w yields strong fit with performance in limited cases (e.g., error rates when comparing perceptual magnitudes), the usefulness of w is quickly exhausted – for instance, when considering individual differences or cases in which high accuracy rates are expected.

Interpretations

The most common interpretation given to both numerical distance and ratio effects (including w) is that of representational precision. In this view, distance/ratio effects arise because the representations of numerically close numbers are more likely to overlap than are those of numerically distant numbers (Dehaene and Changeux, 1993; Verguts and Fias, 2004; Nieder and Dehaene, 2009). Greater representational overlap makes it more difficult to distinguish between two numbers; for instance, when deciding which of the two numbers is numerically greater in a comparison task, or detecting numerical change in an adaptation or looking-time paradigm. This account explains the distance effect because the representations of 5 and 6 overlap to a greater degree than do those of 3 and 8. The ratio effect is accounted for by the assumption that the representations of larger numbers overlap to a greater degree than do smaller numbers; hence, while 8 and 9 overlap to a greater extent than do 7 and 9 (distance effect), 8 and 9 also overlap to a greater extent than do 2 and 3 (ratio effect).

Empirical justification for these assumptions has arisen primarily from work with perceptual magnitudes (e.g., estimating – without explicitly counting – the number of dots in an array, or which of the two arrays of dots contains more dots; Indow and Ida, 1977). Nieder and colleagues (for a review, see Nieder, 2005) recorded single-cell activity from individual prefrontal and parietal neurons in macaque monkeys while monkeys briefly held a quantity of dots in active memory. The authors found that some of the neurons thus sampled were tuned to specific quantities of dots. For instance, a given neuron might be most active (measured in terms of action-potential spike density) when the monkey temporarily held in memory three dots. Interestingly, the neuron would also fire when the monkey held in mind two or four dots; however, the net amount of activity was less than for the preferred quantity (three, in this example), and activity was still less for one or five dots. In this way, Nieder and colleagues showed that there are numerically tuned neurons in the brain, and that these representations are systematically imprecise (i.e., analog). Neuronal responses to different numbers overlap with one another (implying a degree of representational imprecision), and this overlap varies systematically as a function of the numerical distance between them (see **Figure 1** for a simulated example based on human data in Merten and Nieder, 2009). Furthermore, both the neuronal evidence discussed above as well as behavioral evidence in humans (e.g., Nieder and Merten, 2007; Merten and Nieder, 2009) show that numerosity and tuning width are positively correlated. Specifically, as the preferred number increases, the width (i.e., systematic imprecision) of that preference also increases (note that this width is in fact constant on a log–log plot). This means that 8 and 9 will overlap more than 2 and 3, which, as discussed

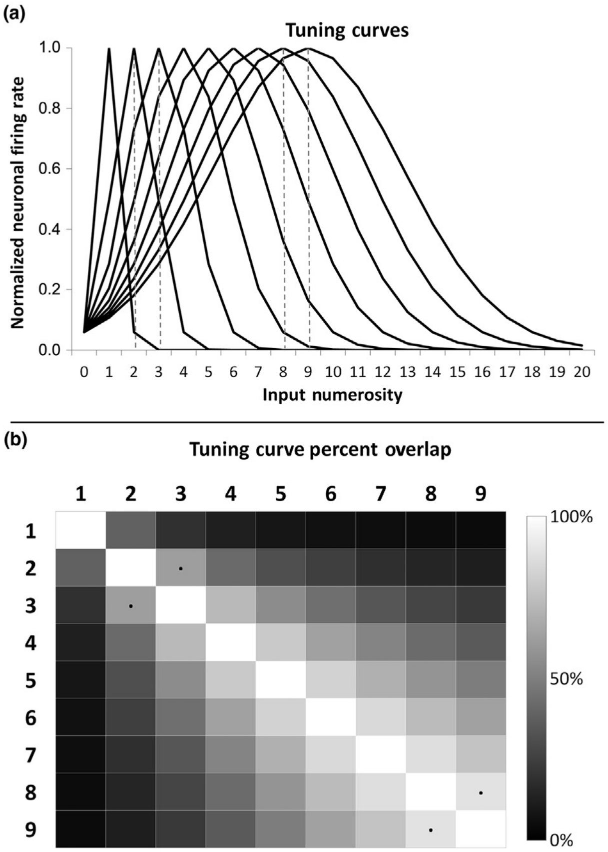

Figure 1 (a) Shows simulated tuning curves based on monkey neuronal data (for a review, see Nieder, 2005) and human and monkey behavioral data (Merten and Nieder, 2009). The *x*-axis is the number of dots in the stimulus, and the *y*-axis is the simulated firing rate. Each curve shows the simulated firing rate for a neuron that is tuned to the number over which it is centered (dashed lines are provided to help identify the curves for 2, 3, 8, and 9). That is, the relative firing rate for a neuron tuned to 9 fires maximally for 9 dots. Notice that this simulated '9-neuron' also fires for 8 dots, but a bit less so than for 9; indeed the firing rate falls off as the presented number of dots (*x*-axis) increasingly differs from 9. Finally, notice that these curves fall off more steeply for neurons tuned to smaller numbers. It is in this way that the width of tuning curves is positively correlated with the number being represented. (b) Plots the degree to which each pair of curves overlap with one another: $\frac{n_1 \cap n_2}{n_1 \cup n_2}$. Overlap proportions for 2 and 3 and 8 and 9 are marked with a dot, which demonstrates the ratio effect.

above, is consistent with the numerical ratio effect. Finally, neuroimaging evidence in humans also shows ratio-dependent tuning in parietal cortex – at least for nonsymbolic magnitudes (Piazza et al., 2004).

To briefly summarize, neural evidence is consistent with the interpretation that numerical ratio and distance effects are indicative of an underlying analog magnitude representation: numerically closer numbers show greater representational overlap (distance effect), and this overlap increases as the size of the numbers in question increase (ratio effect). However, the vast majority of this evidence comes from experiments that examined approximate, nonverbal, nonsymbolic, perceptual magnitudes (e.g., dot arrays; hereafter, simply 'nonsymbolic magnitudes'). When we look at symbolic numbers, such as Indo-Arabic numerals, the evidence is not as clear.

For symbolic numbers such as Indo-Arabic numerals, Verguts et al. (2005) proposed an alternative explanation, beginning with the observation that smaller numbers occur with far greater frequency than do larger numbers (both in speech and in written records; Dehaene and Mehler, 1992). Verguts et al. (2005) created a distributed model of number representation with constant representational precision (equally wide tuning curves) for all numbers, but matched number frequency during model training roughly to that reported by Dehaene and Mehler (1992). When performing a standard number comparison task, the model simulated a ratio effect. In other words, to explain the ratio effect, at least for symbolic numbers, one need not assume representational overlap that increases with the number being represented (see also Verguts and Van Opstal, 2005, for empirical verification of this model).

Sasanguie et al. (2011) have since shown that comparison and priming numerical distance effects are uncorrelated. These results essentially force one to choose between comparison and priming distance effects as the 'true' indicator of representational overlap, with the other indexing some other aspect of processing. To this end, Van Opstal et al. (2008) dissociated the notion of a comparison distance effect entirely from the notion of representational overlap. They did so by showing that comparison distance effects obtain for both number and letter comparisons (when asked 'which letter comes later in the alphabet,' participants were slower to compare, e.g., E vs F than C vs H), but the priming distance effect was found only for numbers. Hence, Van Opstal et al. argued that the priming distance effect is the superior index of number representation, and that the comparison distance effect is primarily due to more domain-general mechanisms, such as response mapping.

Another puzzling aspect of symbolic distance effects occurs when participants are asked to judge relative numerical order. Under such task demands, the effect of numerical distance is in fact reversed on trials where the numbers are in the correct order. For example, participants are faster and more accurate when confirming that 4 – 5 – 6 is in order than when confirming that 3 – 5 – 7 is in order (Turconi et al., 2006; Franklin, 2009; Franklin and Jonides, 2009; Lyons and Beilock, 2013). Crucially, no such reversal of the distance effect is found when participants judge the relative order of nonsymbolic perceptual magnitudes (arrays of dots; Lyons and Beilock, 2013). One interpretation is that highly familiar associations between symbolic numbers (e.g., from the counting sequence) in essence trump the standard influence of numerical distance. Regardless of one's interpretation, the reversed ordinal distance effect demonstrates that simply changing task demands can qualitatively alter the influence of numerical distance on performance, which further calls into question the assumption that symbolic numerical distance effects are a straightforward index of symbolic number representation.

In sum, a common interpretation of numerical ratio and distance effects is that they index underlying representational overlap. In the case of nonsymbolic magnitudes (such as dot arrays), empirical evidence strongly supports this interpretation. However, with respect to symbolic number representation, several lines of evidence converge to render this assumption questionable at best.

Biological Origins – Number Sense

As noted above, adult and infant humans are capable of determining which of the two arrays of objects (e.g., dots) contains more items, even without counting (Buckley and Gillman, 1974). Adults' ability to do so depends on the ratio between the relative numbers of items in each of the two arrays – with a typical limit of about $\frac{10}{11}$ (Cantlon and Brannon, 2007). This pattern of results is robust across cultures and obtains even in individuals whom possess no words for numbers beyond three or four, or other kinds of formal mathematics (Pica et al., 2004). Individuals both with and without formal math education are capable of adding and subtracting such approximate magnitudes as well (Pica et al., 2004; Barth et al., 2006). The ability to process nonsymbolic magnitudes is commonly referred to as 'number sense' (Dehaene, 1997).

Number Sense across Species

When estimating changes in nonsymbolic magnitude, humans and (rhesus macaque) monkeys show a similar pattern of behavior (Merten and Nieder, 2009). A common experimental paradigm used to train and record neural and behavioral responses in monkeys is often referred to as 'delayed match-to-sample,' and it is similar to dot comparison tasks described previously. The difference is that arrays are presented sequentially. An individual sees a single array of dots, which is followed shortly thereafter by a second array. One's task is to determine if the second array matches the first in terms of the number of dots. The benefit of this approach is that one can more transparently record (and hence model) the performance function ('tuning curve') for a specific number – i.e., the first number presented and held in mind during the delay period. (In a standard number comparison task where both numbers are presented simultaneously, it is unclear whether performance and/or neural activity reflects the representation of one number, both numbers, the comparison process, or some combination of all three.) For a specific quantity of dots (e.g., 30), one can plot the probability of a 'same' judgment as a function of the quantity of dots in the second array. Even for quantities as high as 30, both monkeys and adult humans reliably report 'same' most often when indeed the second array contained 30 dots. This demonstrates that both species are capable of processing nonsymbolic magnitudes. Moreover, as the number of dots in the second array shifts away from 30, the probability of a 'same' response decreases systematically as a function of the numerical ratio of the two arrays. In other words, the closer the ratio between the two arrays is to 1, the more likely an individual is to perceive the two arrays as in fact containing the same number of items (thus demonstrating, in both species, the ratio effect, as discussed previously). Interestingly, the function that best describes the decrease in the probability of a 'same' response corresponds to a positively skewed distribution whose overall width increases as the target quantity (the first array) increases (somewhat akin to the curves plotted in **Figure 1**). That is, one can imagine a quasi-normal distribution centered on the target quantity, with a stretched out tail to the right, and a relatively compact tail to the left. Furthermore, the distribution (in both directions) centered on 30 will be wider than that for 25, and that for 25 will be wider for 20, and so on. Interestingly, the function that describes this tuning is quite similar in both humans and monkeys, which suggests a potential common mechanism across species, at least for detecting change in nonsymbolic magnitudes. (Plotted on a linear scale, the distribution widens at a rate of about 0.421 units per unit increase in the target number. On a log-scale, distribution widths are both symmetrical and constant with target number change (Merten and Nieder, 2009).)

The similarity between human and monkey processing of nonsymbolic magnitudes extends to other nonsymbolic magnitudes tasks, such as simultaneous nonsymbolic comparison (Brannon and Terrace, 2002), nonsymbolic ordering (Cantlon and Brannon, 2006), and nonsymbolic arithmetic (Cantlon and Brannon, 2007). Indeed, this ability is common to many species, including dolphins, macaques, capuchins, baboons, wolves, canids, mice, parrots, crows, robins, bees, fish, and even beetles (Agrillo et al., 2009; Armstrong et al., 2012; Baker et al., 2012; Barnard et al., 2013; Beran et al., 2012; Carazo et al., 2012; Nieder, 2005; Pepperberg, 2013; Piffer et al., 2013; Smirnova et al., 2000; Utrata et al., 2012; Yaman et al., 2012 – for reviews, see Agrillo and Beran, 2013; Pahl et al., 2013). In sum, it is clear that the ability to process nonsymbolic magnitudes is not unique to humans, and it is surmised that our ability to do so is part of an innate capacity with deep evolutionary roots (Hubbard et al., 2008).

Number Sense in Early Development

The ability to distinguish visual (Xu and Spelke, 2000) and auditory (Lipton and Spelke, 2003) nonsymbolic magnitudes is present in children as young as 6 months of age. The topography of neural signatures can distinguish between neural pathways related to object identification and nonsymbolic magnitudes; further, this topography is similar in adults, 4-year-olds, and 3-month-old infants, with sensitivity to magnitude centered on the IPS (Cantlon et al., 2006; Izard et al., 2008). Combined with the observation that something akin to a number sense is present across a range of species, the results from human developmental studies suggest that the basis of humans' ability to process nonsymbolic magnitudes is present from a very early developmental stage, does not require formal math training, and may even be innate (Feigenson et al., 2004; Cordes and Brannon, 2008; Nieder and Dehaene, 2009).

This insight has led various researchers to hypothesize that children's number sense forms the foundation on which more sophisticated, culturally acquired mathematical skills rest (e.g., Dehaene, 1997). Indeed, over a dozen papers in the last several years have demonstrated a correlation between individual differences in adults', children's, and even infants' ability to process nonsymbolic magnitudes with performance on a wide range of formal math achievement tests (Bonny and Lourenco, 2013; Desoete et al., 2012; Gilmore et al., 2010; Halberda et al., 2008, 2012; Libertus et al., 2011, 2012, 2013; Lonnemanna et al., 2011; Lourenco et al., 2012; Lyons and Beilock, 2011; Mazzocco et al., 2011a,b; Piazza et al., 2010; Starr et al., 2013; for a review, see Feigenson et al., 2013). Training on approximate arithmetic (using dot arrays) has also been shown to preferentially improve symbolic math achievement scores (Park and Brannon, 2013, 2014; Hyde et al., 2014). These results point to the exciting prospect that numerical cognition may be a prime example of how evolutionarily ancient neural systems are co-opted by cultural inputs (number symbols) to serve a cognitive ability (mathematics) that is crucial to much of modern human life (Dehaene and Cohen, 2007).

On the other hand, it remains unclear precisely how this process occurs. With respect to training, other studies have shown that training on dot comparison tasks does not improve symbolic math scores (Wilson et al., 2006; Dewind and Brannon, 2012; Park and Brannon, 2014); thus, it is not so much improved processing of nonsymbolic magnitudes per se, but improved manipulation of those magnitudes in a mathematical context (arithmetic) that improves symbolic math performance (Park and Brannon, 2014). With respect to individual differences, the relation between nonsymbolic magnitude processing and math achievement has not replicated consistently (De Smedt et al., 2013), and a recent meta-analysis has shown that the relation between nonsymbolic magnitude processing and math achievement is relatively small ($r = 0.20$ for cross-sectional, and $r = 0.17$ for longitudinal studies; Chen and Li, 2014). Moreover, multiple studies have now shown that this correlation is often entirely eliminated once one controls for basic symbolic number processing abilities (such as number comparison, counting, or number ordering; Bartelet et al., 2014; Castronovo and Göbel, 2012; Fuhs and McNeil, 2013; Göbel et al., 2014; Holloway and Ansari, 2009; Kolkman et al., 2013; Lyons and Beilock, 2011, 2014; Sasanguie et al., 2013; Toll and Van Luit, 2014). In other words, the processing of number symbols appears to be more directly tied to more complex math processing (even after controlling for the fact that both are typically in the same visual format; e.g., Lyons and Beilock, 2011; Lyons et al., 2014).

The critical outstanding question, then, may be to understand precisely how nonsymbolic magnitudes aid young children as they first begin learning to comprehend and manipulate numerical symbols in mathematically meaningful ways. However, even in kindergarteners and preschoolers, the current literature remains mixed. For instance, contrast results confirming a relation between nonsymbolic and symbolic number processing in kindergarten or younger (Bonny and Lourenco, 2013; Jordan et al., 2009; Gilmore et al., 2010; Libertus et al., 2013; Mazzocco et al., 2011b; Starr et al., 2013) with results from studies showing largely the opposite (Bartelet et al., 2014; Fuhs and McNeil, 2013; Kolkman et al., 2013; Sasanguie et al., 2014; Toll and Van Luit, 2014). Indeed, there is even evidence to suggest that developmental influence runs in the opposite direction – that improvement in symbolic number abilities predict later accuracy in nonsymbolic magnitude comparison (Mussolin et al., 2014; see also Gelman and Gallistel, 2004). It may be that taking a broader view of how the key neural systems of young children change as a function of math education and math learning can provide crucial insight into this debate.

Number or Magnitude?

At this point, the reader may have noticed that I have used the term 'magnitude' when discussing the capacity to process approximate, nonverbal, perceptual, and nonsymbolic numbers or quantities. In recent years, the phrase 'approximate number system' (ANS) has appeared as an appellation for one's capacity to perform many of the nonsymbolic tasks described above (e.g., Halberda et al., 2006; Butterworth, 2010; Cantlon et al., 2009; McCrink and Spelke, 2010; Piazza, 2010). References to the ANS have become common in the literature; however, this has not occurred without some controversy. First, the scope of the term is not entirely clear, as it has been used refer to a range of tasks which are perhaps less consistently related to one another than might be expected if all relied upon a singular and unitary underlying construct (Gilmore et al., 2011; Inglis and Gilmore, 2014; though see also Price et al., 2012). Second, there remains some question as to whether what is being measured by these nonsymbolic tasks is indeed *numerical*.

This latter point of controversy is driven less by conflicting results than by a fundamental measurement limit: it is geometrically impossible to make all nonnumerical parameters strictly uncorrelated with number in a single trial. Take, for example, a nonsymbolic comparison task. On a given trial, one will see two dot arrays, usually arranged side-by-side. The task is to determine which array contains more items. Here, 'number' is conceptualized as the sum of the discrete items in a given array, and this is contrasted with continuous visual properties of the stimulus, such as individual dot size (area), the total area of all dots in a given array, the local spacing (Euclidean distance) between individual dots, global spacing (e.g., the average pairwise distance between all pairs of dots in the array – a property closely related to density), the outer contour length of the array (a semisubjective tracing of the outer envelope of the array), and so on. In contrast to a discrete conception of number, these properties vary continuously (akin to how the amount of water in a glass varies continuously, at least to the unaided human eye), and hence are typically labeled as 'magnitudes' as opposed to numbers. Notice that most of these properties will tend to be correlated (or sometimes anticorrelated) with the relative number of dots in each array; that is, these continuous properties provide information about relative number. Hence, decisions may be made not on the basis of the number of items in each array, but may instead be driven entirely or in part by one or more of these covariate, continuous parameters. For instance, if the size of the individual dots is held constant, the array with a greater total area must contain more dots; if total area is equated across arrays, then the array with smaller dots on average must contain more dots. Analogous trade-offs present themselves for the other continuous properties as well. In sum, the very rules of geometry preclude the construction of a pair of arrays that differ in number of items and are exactly equal on all conceivable continuous (nonnumerical) parameters. The question, then, is, if we have no way to measure number independently of these other confounding variables, then can we ever be certain that what we are calling 'approximate number' is numerical at all? Might it be more appropriate to refer to an 'approximate magnitude system'? Indeed, one may question the logical soundness of an 'approximate number' to begin with, in that one may simply be confusing a property of a set (the number of items in the set) with the set's capacity for change (i.e., the possibility for the set to contain different numbers of objects with different probabilities). Indeed, this distinction is crucial for understanding and maintaining the difference between a number (even a number expressed as a ratio or proportion) and a probability. To be sure, debate is heated (e.g., Cordes and Brannon, 2009; De Hevia, 2011; Gebuis and Reynvoet, 2012a,b,c; Leibovich and Henik, 2013, 2014; Nys and Content, 2012); however, as has happened elsewhere when scientists have run up against what appears to be a fundamental limit on humans' capacity to measure a given phenomenon, one's ultimate conclusion may well be more a matter of philosophy (Heisenberg, 1979).

In sum, then, whether one chooses to refer to an 'ANS,' an 'approximate magnitude system,' 'number sense,' or simply 'nonsymbolic magnitude processing' may, at least at present, be largely a matter of opinion. Given the ongoing controversy, for present purposes, I have chosen what seems to me the most neutral term – nonsymbolic magnitude processing. However, the reader is encouraged to recognize these other terms in the literature, and, hopefully, consider the theoretical assumptions behind each.

Subitizing

As noted in the previous section, there is a certain conceptual difficulty (and perhaps methodological indeterminacy) with the notion of 'approximate number.' If one's requirement for nonsymbolic 'number' is that the numerical representation be exact, then one possible candidate is subitizing. Subitizing refers to the rapid, exact apprehension of the number of objects in a set without explicit counting (Mandler and Shebo, 1982; Dehaene and Cohen, 1994; Trick and Pylyshyn, 1994). Subitizing is subject to a limit of about four items that appear to be tied to a general processing capacity limit for visual short-term memory (Luck and Vogel, 1997; Piazza et al., 2011). When enumerating the exact number of objects in a set, when there are four or fewer, performance varies very little for sets with one versus four objects (both in terms of errors and response times; e.g., Trick and Pylyshyn; Revkin et al., 2008; Vuokko et al., 2013; Watson et al., 2007). This stands in contrast to enumerating larger sets of objects. One either begins to introduce increasingly large errors as the number of items increases (in the case of estimation; e.g., Revkin et al., 2008; Izard and Dehaene, 2008), or response times systematically increase as one counts the additional items (e.g., Trick and Pylyshyn, 1994; Vuokko et al., 2013). Furthermore, counting appears to rely disproportionately more on working memory resources than does subitizing (Shimomura and Kumada, 2011; Tuholski et al., 2001). Neuroimaging evidence also supports the notion that processing nonsymbolic sets >4 relies on qualitatively different neural systems than does processing subitizable set ≤ 4 (Ansari et al., 2007; Ester et al., 2012; Sathian et al., 1999; Vetter et al., 2011; Vuokko et al., 2013). There is also evidence to suggest there are two separate systems for processing small (≤ 4) and large (>4) numbers of items even in infants (Xu and Spelke, 2000). Taken together, there is evidence to suggest that subitizing operates in a qualitatively different manner than processing of larger nonsymbolic magnitudes. One important upshot (to which I will return in the next Section Symbolic Numbers) is that representation of exact number appears to be possible in the case of subitizing, even in young children (Le Corre and Carey, 2007).

Symbolic Numbers

Symbolic numbers are a relatively recent cultural invention when viewed from the broader context of human evolution. There is some evidence to suggest that tally sticks were used to record quantities perhaps as early as 40 000 years ago (Ifrah, 2000). However, evidence for more sophisticated systems for representing and manipulating abstract numerical symbols is absent from the archaeological record until the rise of Mesopotamian civilization around 3100 BC, which was followed shortly thereafter by the emergence of symbolic number systems in ancient Egypt and China only a few centuries later (Ifrah, 2000). Archaeological evidence for the use of spoken number words – another kind of number symbol – is more difficult to come by, though one may infer their use, for example, from root languages such as Proto-Indo-European (PIE). Many languages that have descended from PIE share similar forms for number words up to about 10 (Menninger, 1969/1992). As PIE is believed to have been originally spoken *c.*4200 BC (Blench and Spriggs, 1997), one may infer the use of similar number words perhaps as early as roughly 6000 years ago. On the other hand, present-day indigenous cultures without substantial contact with modern developed cultures have number words up to only three or four, and they lack more sophisticated means of computing exact quantities that exceed this limited range (Pica et al., 2004). In sum, while the ability to process nonsymbolic magnitudes appears to stem from a deep evolutionary history, the ability to manipulate exact numbers in symbolic form is a much more recent cultural invention (see also Damerow, 2001). This places the acquisition and mastery of even basic processing of symbolic numbers (such as memorization and linking of simple arithmetic facts) at a fascinating junction between evolution and culture (Dehaene and Cohen, 2007; Ansari, 2008).

Symbol Grounding

A central question for research on symbolic numbers concerns what exactly number symbols represent – what do they refer? (Harnad, 1990). An early proposal is that they refer to the corresponding nonsymbolic magnitude: "When we learn number symbols, we simply attach their arbitrary shapes to the relevant nonsymbolic quantity representations" (Dehaene, 2008: p. 552; see also, Dehaene, 1997; Gallistel and Gelman, 2000). The appeal of this explanation is clear: the meaning of a symbolic number is grounded in what appears to be its evolutionary precursor in the (possibly innate) representation of the corresponding nonsymbolic magnitude, and support for this view has been echoed many times over (e.g., Verguts and Fias, 2004; Feigenson et al., 2004, 2013; Piazza et al., 2007; Hubbard et al., 2008; Libertus and Brannon, 2009; Nieder and Dehaene, 2009; Lyons and Ansari, 2009; Eger et al., 2009). More specifically, the argument is that symbolic numbers provide a more precise mapping (narrower tuning curve) onto the corresponding nonsymbolic magnitude (for a computational instantiation of this view, see Verguts and Fias, 2004).

Three different lines of evidence are often cited to support the proposal that symbolic numbers' meaning is derived from direct reference to their corresponding nonsymbolic magnitude. First, numerical signatures such as the distance and ratio effect show qualitatively similar patterns for symbolic numbers and nonsymbolic magnitudes (e.g., Buckley and Gillman, 1974; Dehaene, 2008). Second, neuroimaging evidence often points to similar neural substrates – specifically, the IPS – for symbolic and nonsymbolic number processing (Fias et al., 2003; Diester and Nieder, 2007; Piazza et al., 2007; Eger et al., 2009). Third, individual differences in nonsymbolic magnitude processing are related to more complex symbolic math abilities (as reviewed in the previous Section Number Sense in Early Development). In sum, one candidate for the meaning of a symbolic numbers – i.e., a potential solution to the symbol grounding problem – is that a given symbol simply refers to one's internal representation of the corresponding nonsymbolic magnitude.

Recently, several counterarguments to this proposal have arisen. First, one may note that distance effects are observed in virtually any discrimination task, whether one is distinguishing between items on the basis of perceptual dimensions (e.g., odor discrimination in drosophila; Parnas et al., 2013) or more abstract, categorical variables (e.g., distinguishing between species of animal figures; Gilbert et al., 2008). As discussed previously when interpreting distance and ratio effects, it is difficult to see how these effects in symbolic numbers are indicative of underlying representations in the same way as nonsymbolic magnitudes. Hence, it may be just as problematic to argue that qualitatively similar numerical distance/ratio effects are evidence of common representation across symbolic numbers and nonsymbolic magnitudes as it would be to argue that odors in drosophila and abstract animal categories in humans are underlain by a common representation.

Second, with respect to neural overlap of symbolic and nonsymbolic number processing, inferring a common neural mechanism from coactivation of brain regions (called reverse inference), though common, is logically problematic (Poldrack, 2006). Recent evidence suggests that such overlap in the case of numbers is dependent upon task demands in any case: neural activity for symbolic and nonsymbolic numerical ordering tasks shows a qualitatively different pattern of overlap relative to that for symbolic and nonsymbolic numerical comparison tasks (Lyons and Beilock, 2013). Further, of the three papers (Eger et al., 2009; Damarla and Just, 2013; Bulthé et al., 2014) that assessed whether distributed patterns of activity during processing of numbers in one format (e.g., symbolic) can be used to decode processing of numbers in the opposite format (e.g., nonsymbolic), only one (Eger et al., 2009) found evidence of successful cross-format decoding (and even in that case decoding was unidirectional and only slightly above chance: 57% accuracy, where chance was 50%). Cross-format fMRI adaptation has also yielded mixed results, with the responses to format change substantially larger than the responses to number change (Cohen Kadosh et al., 2011; though see also Piazza et al., 2007). In sum, while it is certainly possible that neural overlap of symbolic numbers and nonsymbolic magnitudes is more than a coincidence (Dehaene and Cohen, 2007), closer inspection suggests that there is substantial neural dissociation between the two formats. Behavioral evidence is consistent with this view: when asked to directly compare a symbolic number with a nonsymbolic magnitude (in an otherwise standard number comparison task), the cost of switching between formats is closer to what one would expect if the two formats referenced different as opposed to the same underlying representations (Lyons et al., 2012).

Third, with respect to the relationship between nonsymbolic magnitude processing and more complex math skills, as discussed in the previous Section Number Sense in Early Development, evidence for this result is quite mixed, even in preschoolers and kindergarteners who are just learning to use symbolic numbers. In sum, then, recent evidence has begun to erode a strong view of the notion that the meanings of number symbols are grounded in a direct reference to their nonsymbolic counterparts. An alternative explanation is that number symbols are initially linked exclusively via the exact, nonsymbolic quantities within the subitizing range (≤ 4; Carey, 2004). Indeed, Le Corre and Carey (2007) showed that 3- and 4-year-old children mapped number words onto corresponding magnitudes within the subitizing range prior to acquiring an understanding of the 'cardinality principle' (that counting to any number yields the number in the set, as indexed as the last number said). Children at this age failed to consistently map corresponding number words onto sets containing more than four items until several months after acquiring the cardinality principle. Further evidence consistent with this view has been found in adults: the cost of mixing symbolic and nonsymbolic formats for small numbers ($\leq$4) is substantially smaller than that found for large numbers (>4; Lyons et al., 2012), suggesting that subitizable symbolic and nonsymbolic numbers may retain a strong link even into adulthood.

Beyond Number Sense

How, then, do number symbols outside the subitizing range acquire meaning? One idea is that, having established a one-to-one mapping with nonsymbolic subitizable magnitudes, the meaning of (numerically) larger symbolic numbers are then bootstrapped from the smaller number symbols (Carey, 2004). Precisely how this process occurs, however, remains a point of debate (Ansari, 2008). One proposal is that the grammatical structure of language plays a critical role in inferring the existence and later the meaning of large exact numbers (Carey, 2004; Le Corre and Carey, 2007; Almoammer et al., 2013; Sarnecka et al., 2007; Sullivan and Barner, 2014). Another possibility is that mapping symbolic numbers to a visual-spatial mental number line is key (e.g., Gunderson et al., 2012). Specifically, understanding that the numerical distance between integers remains constant helps one to apprehend the notion of large exact numbers, which is evidenced by a linearization of the number line up to ever-increasing magnitudes (10, 100, 1000, etc.; Siegler and Ramani, 2008). Yet another view suggests that how we understand numbers as ordered sequences differs fundamentally between symbolic and nonsymbolic numbers (Lyons and Beilock, 2011, 2013). The ordinal associations between symbolic numbers may thus provide one distinct aspect of symbolic numbers' respective meaning (Nieder, 2009). These competing views need not be mutually exclusive, and indeed, they all share the general assumption that the meanings of larger number symbols do not remain directly tied to their nonsymbolic counterpart. (For a competing view that expressly disagrees with this assumption, see Feigenson et al. (2013).) Note that this assumption is consistent with a broader view of symbolic representation more generally (Deacon, 1997; for an early suggestion applying this perspective specifically to number representation, see Nieder, 2009). According to this view, it is the relations between symbols that ultimately come to define a symbolic system. Over time, these relations may even come to overshadow each symbol's link to an external referent. It is perhaps this that makes it possible to manipulate very large numbers such as 1 000 000 without having a concrete sense of what 1 000 000 is like. That said, even if such a view proves to be correct, a major unanswered question concerns the precise mechanism – whether that be linguistic, visual-spatial, ordinal, nonsymbolic magnitudes, some combination thereof, or something else entirely – that links number symbols to one another. Answering this question is thus a major contemporary topic of research in the field of numerical cognition. On a somewhat grander scale, such research can help us understand how cultural and evolutionary forces interact within the human brain in shaping our ability to manipulate the world of and with mathematics.

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See also: Cognitive Development: Mathematics Learning and Instruction; Mathematical Concepts During Early Childhood Across Cultures, Development of; Mathematics Education; Number Systems, Evolution of; Number, Grammatical; Parietal Lobe; Serial Order, Representation of.

Bibliography

Agrillo, C., Beran, M.J., 2013. Number without language: comparative psychology and the evolution of numerical cognition. Frontiers in Psychology 4, 295.

Agrillo, C., Dadda, M., Serena, G., Bisazza, A., 2009. Use of number by fish. PLoS One 4 (3), e4786.

Almoammer, A., Sullivan, J., Donlan, C., Marušič, F., Žaucer, R., O'Donnell, T., Barner, D., 2013. Grammatical morphology as a source of early number word meanings. Proceedings of the National Academy of Sciences of the United States of America 110 (46), 18448–18453.

Ansari, D., Fugelsang, J.A., Dhital, B., Venkatraman, V., 2006. Dissociating response conflict from numerical magnitude processing in the brain: an event-related fMRI study. NeuroImage 32 (2), 799–805.

Ansari, D., Lyons, I.M., van Eimeren, L., Xu, F., 2007. Linking visual attention and number processing in the brain: the role of the temporo-parietal junction in small and large symbolic and nonsymbolic number comparison. Journal of Cognitive Neuroscience 19 (11), 1845–1853.

Ansari, D., 2008. Effects of development and enculturation on number representation in the brain. Nature Reviews Neuroscience 9 (4), 278–291.

Armstrong, N., Garland, A., Burns, K.C., 2012. Memory for multiple cache locations and prey quantities in a food-hoarding songbird. Frontiers in Psychology 3, 584.

Baker, J.M., Morath, J., Rodzon, K.S., Jordan, K.E., 2012. A shared system of representation governing quantity discrimination in canids. Frontiers in Psychology 3, 387.

Barnard, A.M., Hughes, K.D., Gerhardt, R.R., Divincenti Jr., L., Bovee, J.M., Cantlon, J.F., 2013. Inherently analog quantity representations in olive baboons (*Papio anubis*). Frontiers in Psychology 4, 253.

Bartelet, D., Vaessen, A., Blomert, L., Ansari, D., 2014. What basic number processing measures in kindergarten explain unique variability in first-grade arithmetic proficiency? Journal of Experimental Child Psychology 117, 12–28.

Barth, H., La Mont, K., Lipton, J., Dehaene, S., Kanwisher, N., Spelke, E., 2006. Non-symbolic arithmetic in adults and young children. Cognition 98 (3), 199–222.

Beran, M.J., Perdue, B.M., Parrish, A.E., Evans, T.A., 2012. Do social conditions affect capuchin monkeys' (*Cebus apella*) choices in a quantity judgment task? Frontiers in Psychology 3, 492.

Blench, R., Spriggs, M. (Eds.), 1997. Archaeology and Language III: Artefacts, Languages and Texts. Routledge, New York.

Bonny, J.W., Lourenco, S.F., 2013. The approximate number system and its relation to early math achievement: evidence from the preschool years. Journal of Experimental Child Psychology 114 (3), 375–388.

Brannon, E.M., Terrace, H.S., 2002. The evolution and ontogeny of ordinal numerical ability. In: Bekoff, M., Allen, C., Burghardt, G. (Eds.), The Cognitive Animal: Empirical and Theoretical Perspectives on Animal Cognition. MIT Press, Cambridge, MA, pp. 197–204.

Buckley, P.B., Gillman, C.B., 1974. Comparisons of digits and dot patterns. Journal of Experimental Psychology 103 (6), 1131–1136.

Bulthé, J., De Smedt, B., Op de Beeck, H.P., 2014. Format-dependent representations of symbolic and non-symbolic numbers in the human cortex as revealed by multi-voxel pattern analyses. NeuroImage 87, 311–322.

Butterworth, B., 2010. Foundational numerical capacities and the origins of dyscalculia. Trends in Cognitive Sciences 14 (12), 534–541.

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., Brannon, E.M., 2006. Shared system for ordering small and large numbers in monkeys and humans. Psychological Science 17 (5), 401–406.

Cantlon, J.F., Brannon, E.M., 2007. Basic math in monkeys and college students. PLoS Biology 5 (12), e328.

Cantlon, J.F., Platt, M.L., Brannon, E.M., 2009. Beyond the number domain. Trends in Cognitive Sciences 13 (2), 83–91.
Carazo, P., FernÃ¡ndez-Perea, R., Font, E., 2012. Quantity estimation based on numerical cues in the mealworm beetle (*Tenebrio molitor*). Frontiers in Psychology 3, 502.
Carey, S., Winter 2004. Bootstrapping and the origins of concepts. Daedalus 59–68.
Castronovo, J., Göbel, S.M., 2012. Impact of high mathematics education on the number sense. PLoS One 7 (4), e33832.
Chen, Q., Li, J., 2014. Association between individual differences in non-symbolic number acuity and math performance: a meta-analysis. Acta Psychologica (Amst) 148, 163–172.
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.
Cordes, S., Brannon, E.M., 2008. Quantitative competencies in infancy. Developmental Science 11 (6), 803–808.
Cordes, S., Brannon, E.M., 2009. The relative salience of discrete and continuous quantity in young infants. Developmental Science 12 (3), 453–463.
Damarla, S.R., Just, M.A., 2013. Decoding the representation of numerical values from brain activation patterns. Human Brain Mapping 34 (10), 2624–2634.
Damerow, P., 2001. Evolution of number systems. In: Smelser, N.J., Baltes, P.B. (Eds.), International Encyclopedia of Social and Behavioral Sciences, pp. 10753–10756.
Deacon, T., 1997. The Symbolic Species: The Co-evolution of Language and the Brain. W.W. Norton & Company, Inc., New York.
Dehaene, S., 1997. The Number Sense: How the Mind Creates Mathematics. Oxford University Press, New York.
Dehaene, S., Mehler, J., 1992. Cross-linguistic regularities in the frequency of number words. Cognition 43 (1), 1–29.
Dehaene, S., Changeux, J.P., 1993. Development of elementary numerical abilities: a neuronal model. Journal of Cognitive Neuroscience 5 (4), 390–407.
Dehaene, S., Cohen, L., 1994. Dissociable mechanisms of subitizing and counting: neuropsychological evidence from simultanagnosic patients. Journal of Experimental Psychology Human Perception and Performance 20 (5), 958–975.
Dehaene, S., Cohen, L., 2007. Cultural recycling of cortical maps. Neuron 56 (2), 384–398.
Dehaene, S., 2008. Symbols and quantities in parietal cortex: elements of a mathematical theory of number representation and manipulation. In: Haggard, P., Rossetti, Y. (Eds.), Sensorimotor Foundations of Higher Cognition (Attention and Performance). Oxford University Press, New York, pp. 527–574.
De Hevia, M.D., 2011. Sensitivity to number: reply to Gebuis and Gevers. Cognition 121 (2), 253–255.
De Smedt, B., Noël, M.P., Gilmore, C., Ansari, D., 2013. How do symbolic and non-symbolic numerical magnitude processing skills relate to individual differences in children's mathematical skills? A review of evidence from brain and behavior. Trends in Neuroscience and Education 2 (2), 48–55.
Desoete, A., Ceulemans, A., De Weerdt, F., Pieters, S., 2012. Can we predict mathematical learning disabilities from symbolic and non-symbolic comparison tasks in kindergarten? Findings from a longitudinal study. British Journal of Educational Psychology 82 (1), 64–81.
Dewind, N.K., Brannon, E.M., 2012. Malleability of the approximate number system: effects of feedback and training. Frontiers in Human Neuroscience 6, 68.
Diester, I., Nieder, A., 2007. Semantic associations between signs and numerical categories in the prefrontal cortex. PLoS Biology 5, e294.
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.
Ester, E.F., Drew, T., Klee, D., Vogel, E.K., Awh, E., 2012. Neural measures reveal a fixed item limit in subitizing. Journal of Neuroscience 32 (21), 7169–7177.
Feigenson, L., Dehaene, S., Spelke, E., 2004. Core systems of number. Trends in Cognitive Sciences 8 (7), 307–314.
Feigenson, L., Libertus, M.E., Halberda, J., 2013. Links between the intuitive sense of number and formal mathematics ability. Child Development Perspectives 7 (2), 74–79.
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.
Franklin, M.S., Jonides, J., Smith, E.E., 2009. Processing of order information for numbers and months. Memory and Cognition 37 (5), 644–654.
Franklin, M.S., Jonides, J., 2009. Order and magnitude share a common representation in parietal cortex. Journal of Cognitive Neuroscience 21 (11), 2114–2120.
Fuhs, M.W., McNeil, N.M., 2013. ANS acuity and mathematics ability in preschoolers from low-income homes: contributions of inhibitory control. Developmental Science 16 (1), 136–148.
Gallistel, C.R., Gelman, R., 2000. Non-verbal numerical cognition: from reals to integers. Trends in Cognitive Sciences 4 (2), 59–65.
Gebuis, T., Reynvoet, B., 2012a. Continuous visual properties explain neural responses to nonsymbolic number. Psychophysiology 49 (11), 1481–1491.
Gebuis, T., Reynvoet, B., 2012b. The interplay between nonsymbolic number and its continuous visual properties. Journal of Experimental Psychology General 141 (4), 642–648.
Gebuis, T., Reynvoet, B., 2012c. The role of visual information in numerosity estimation. PLoS One 7 (5), e37426.
Gelman, R., Gallistel, C.R., 2004. Language and the origin of numerical concepts. Science 306 (5695), 441–443.
Gilbert, A.L., Regier, T., Kay, P., Ivry, R.B., 2008. Support for lateralization of the Whorf effect beyond the realm of color discrimination. Brain and Language 105 (2), 91–98.
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.
Gilmore, C., Attridge, N., Inglis, M., 2011. Measuring the approximate number system. Quarterly Journal of Experimental Psychology (Hove) 64 (11), 2099–2109.
Göbel, S.M., Watson, S.E., Lervåg, A., Hulme, C., 2014. Children's arithmetic development: it is number knowledge, not the approximate number sense, that counts. Psychological Science 25 (3), 789–798.
Grill-Spector, K., Henson, R., Martin, A., 2006. Repetition and the brain: neural models of stimulus-specific effects. Trends in Cognitive Sciences 10 (1), 14–23.
Gunderson, E.A., Ramirez, G., Beilock, S.L., Levine, S.C., 2012. The relation between spatial skill and early number knowledge: the role of the linear number line. Developmental Psychology 48 (5), 1229–1241.
Halberda, J., Sires, S.F., Feigenson, L., 2006. Multiple spatially overlapping sets can be enumerated in parallel. Psychological Science 17 (7), 572–576.
Halberda, J., Feigenson, L., 2008. Developmental change in the acuity of the number sense: the approximate number system in 3-, 4-, 5- and 6-year-olds and adults. Developmental Psychology 44 (5), 1457–1465.
Halberda, J., Ly, R., Wilmer, J.B., Naiman, D.Q., Germine, L., 2012. Number sense across the lifespan as revealed by a massive internet-based sample. Proceedings of the National Academy of Sciences of the United States of America 109 (28), 11116–11120.
Halberda, J., Mazzocco, M.M., Feigenson, L., 2008. Individual differences in non-verbal number acuity correlate with maths achievement. Nature 455 (7213), 665–668.
Harnad, S., 1990. The symbol grounding problem. Physica D Nonlinear Phenomena 42, 335–346.
Heisenberg, W., 1979. Philosophical Problems of Quantum Physics. Oxbow Press, Oxford.
Holloway, I.D., Ansari, D., 2009. Mapping numerical magnitudes onto symbols: the numerical distance effect and individual differences in children's mathematics achievement. Journal of Experimental Child Psychology 103 (1), 17–29.
Holloway, I.D., Battista, C., Vogel, S.E., Ansari, D., 2013. Semantic and perceptual processing of number symbols: evidence from a cross-linguistic fMRI adaptation study. Journal of Cognitive Neuroscience 25 (3), 388–400.
Hubbard, E.M., Diester, I., Cantlon, J.F., Ansari, D., Opstal, F.V., Troiani, V., 2008. The evolution of numerical cognition: from number neurons to linguistic quantifiers. Journal of Neuroscience 28 (46), 11819–11824.
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.
Ifrah, G., 2000. The Universal History of Numbers: From Prehistory to the Invention of the Computer. John Wiley & Sons, Inc., New York.
Indow, T., Ida, M., 1977. Scaling of dot numerosity. Perception & Psychophysics 22 (3), 265–276.
Inglis, M., Gilmore, C., 2014. Indexing the approximate number system. Acta Psychologica (Amst) 145, 147–155.
Izard, V., Dehaene, S., 2008. Calibrating the mental number line. Cognition 106 (3), 1221–1247.
Izard, V., Dehaene-Lambertz, G., Dehaene, S., 2008. Distinct cerebral pathways for object identity and number in human infants. PLoS Biology 6 (2), e11.
Jordan, N.C., Kaplan, D., Ramineni, C., Locuniak, M.N., 2009. Early math matters: kindergarten number competence and later mathematics outcomes. Developmental Psychology 45 (3), 850–867.
Kaufmann, L., Koppelstaetter, F., Delazer, M., Siedentopf, C., Rhomberg, P., Golaszewski, S., Felber, S., Ischebeck, A., 2005. Neural correlates of distance and congruity effects in a numerical Stroop task: an event-related fMRI study. NeuroImage 25 (3), 888–898.
Kolkman, M.E., Kroesbergen, E.H., Leseman, P.P.M., 2013. Early numerical development and the role of non-symbolic and symbolic skills. Learning and Instruction 25, 95–103.

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.

Leibovich, T., Henik, A., 2014. Comparing performance in discrete and continuous comparison tasks. Quarterly Journal of Experimental Psychology (Hove) 67 (5), 899–917.

Leibovich, T., Henik, A., 2013. Magnitude processing in non-symbolic stimuli. Frontiers in Psychology 4, 375.

Libertus, M.E., Brannon, E.M., 2009. Behavioral and neural basis of number sense in infancy. Current Directions in Psychological Science 18 (6), 346–351.

Libertus, M.E., Feigenson, L., Halberda, J., 2011. Preschool acuity of the approximate number system correlates with school math ability. Developmental Science 14 (6), 1292–1300.

Libertus, M.E., Odic, D., Halberda, J., 2012. Intuitive sense of number correlates with math scores on college-entrance examination. Acta Psychologica 141 (3), 373–379.

Libertus, M.E., Feigenson, L., Halberda, J., 2013. Is approximate number precision a stable predictor of math ability? Learning and Individual Differences 25, 126–133.

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

Lonnemanna, J., Linkersdörfera, J., Hasselhorna, M., Lindberg, S., 2011. Symbolic and non-symbolic distance effects in children and their connection with arithmetic skills. Journal of Neurolinguistics 24 (5), 582–591.

Lourenco, S.F., Bonny, J.W., Fernandez, E.P., Rao, S., 2012. Nonsymbolic number and cumulative area representations contribute shared and unique variance to symbolic math competence. Proceedings of the National Academy of Sciences of the United States of America 109 (46), 18737–18742.

Luck, S.J., Vogel, E.K., 1997. The capacity of visual working memory for features and conjunctions. Nature 390 (6657), 279–281.

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.

Lyons, I.M., Beilock, S.L., 2009. Beyond quantity: individual differences in working memory and the ordinal understanding of numerical symbols. Cognition 113 (2), 189–204.

Lyons, I.M., Beilock, S.L., 2011. Numerical ordering ability mediates the relation between number-sense and arithmetic competence. Cognition 121 (2), 256–261.

Lyons, I.M., Ansari, D., Beilock, S.L., 2012. Symbolic estrangement: evidence against a strong association between numerical symbols and the quantities they represent. Journal of Experimental Psychology General 141 (4), 635–641.

Lyons, I.M., Beilock, S.L., 2013. Ordinality and the nature of symbolic numbers. Journal of Neuroscience 33 (43), 17052–17061.

Lyons, I.M., Price, G.R., Vaessen, A., Blomert, L., Ansari, D., 2014. Numerical predictors of arithmetic success in grades 1–6. Developmental Science 17 (5), 714–726.

Maloney, E.A., Risko, E.F., Preston, F., Ansari, D., Fugelsang, J., 2010. Challenging the reliability and validity of cognitive measures: the case of the numerical distance effect. Acta Psychologica (Amst) 134 (2), 154–161.

Mandler, G., Shebo, B.J., 1982. Subitizing: an analysis of its component processes. Journal of Experimental Psychology General 111 (1), 1–22.

Mazzocco, M.M., Feigenson, L., Halberda, J., 2011a. Impaired acuity of the approximate number system underlies mathematical learning disability (dyscalculia). Child Development 82 (4), 1224–1237.

Mazzocco, M.M., Feigenson, L., Halberda, J., 2011b. Preschoolers' precision of the approximate number system predicts later school mathematics performance. PLoS One 6 (9), e23749.

McCrink, K., Spelke, E.S., 2010. Core multiplication in childhood. Cognition 116 (2), 204–216.

Menninger, K., 1969/1992. Number Words and Number Symbols: A Cultural History of Numbers. Dover Publications, Inc., New York.

Merten, K., Nieder, A., 2009. Compressed scaling of abstract numerosity representations in adult humans and monkeys. Journal of Cognitive Neuroscience 21 (2), 333–346.

Moyer, R.S., Landauer, T.K., 1967. Time required for judgements of numerical inequality. Nature 215 (5109), 1519–1520.

Mussolin, C., Noël, M.P., Pesenti, M., Grandin, C., De Volder, A.G., 2013. Neural correlates of the numerical distance effect in children. Frontiers in Psychology 4, 663.

Mussolin, C., Nys, J., Content, A., Leybaert, J., 2014. Symbolic number abilities predict later approximate number system acuity in preschool children. PLoS One 9 (3), e91839.

Nieder, A., 2009. Prefrontal cortex and the evolution of symbolic reference. Current Opinion in Neurobiology 19 (1), 99–108.

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

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

Nieder, A., 2005. Counting on neurons: the neurobiology of numerical competence. Nature Reviews Neuroscience 6 (3), 177–190.

Notebaert, K., Pesenti, M., Reynvoet, B., 2010. The neural origin of the priming distance effect: distance-dependent recovery of parietal activation using symbolic magnitudes. Human Brain Mapping 31 (5), 669–677.

Nys, J., Content, A., 2012. Judgement of discrete and continuous quantity in adults: number counts! Quarterly Journal of Experimental Psychology (Hove) 65 (4), 675–690.

Pahl, M., Si, A., Zhang, S., 2013. Numerical cognition in bees and other insects. Frontiers in Psychology 4, 162.

Panteleeva, S., Reznikova, Z., Vygonyailova, O., 2013. Quantity judgments in the context of risk/reward decision making in striped field mice: first count then hunt. Frontiers in Psychology 4, 53.

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

Park, J., Brannon, E.M., 2014. Improving math with number sense training: an investigation of its underlying mechanism. Cognition 133 (1), 188–200.

Parnas, M., Lin, A.C., Huetteroth, W., Miesenböck, G., 2013. Odor discrimination in *Drosophila*: from neural population codes to behavior. Neuron 79 (5), 932–944.

Pepperberg, I.M., 2013. Abstract concepts: data from a grey parrot. Behavioural Processes 93, 82–90.

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.

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

Piazza, M., Facoetti, A., Trussardi, A.N., Berteletti, I., Conte, S., Lucangeli, D., Dehaene, S., Zorzi, M., 2010. Developmental trajectory of number acuity reveals a severe impairment in developmental dyscalculia. Cognition 116 (1), 33–41.

Piazza, M., Fumarola, A., Chinello, A., Melcher, D., 2011. Subitizing reflects visuo-spatial object individuation capacity. Cognition 121 (1), 147–153.

Pica, P., Lemer, C., Izard, V., Dehaene, S., 2004. Exact and approximate arithmetic in an Amazonian indigene group. Science 306 (5695), 499–503.

Piffer, L., Miletto Petrazzini, M.E., Agrillo, C., 2013. Large number discrimination in newborn fish. PLoS One 8 (4), e62466.

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

Poldrack, R.A., 2006. Can cognitive processes be inferred from neuroimaging data? Trends in Cognitive Sciences 10 (2), 59–63.

Price, G.R., Palmer, D., Battista, C., Ansari, D., 2012. Nonsymbolic numerical magnitude comparison: reliability and validity of different task variants and outcome measures, and their relationship to arithmetic achievement in adults. Acta Psychologica 140 (1), 50–57.

Revkin, S.K., Piazza, M., Izard, V., Cohen, L., Dehaene, S., 2008. Does subitizing reflect numerical estimation? Psychological Science 19 (6), 607–614.

Reynvoet, B., Brysbaert, M., Fias, W., 2002. Semantic priming in number naming. Quarterly Journal of Experimental Psychology A 55 (4), 1127–1139.

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.

Rubinsten, O., Henik, A., Berger, A., Shahar-Shalev, S., 2002. The development of internal representations of magnitude and their association with Arabic numerals. Journal of Experimental Child Psychology 81 (1), 74–92.

Sarnecka, B.W., Kamenskaya, V.G., Yamana, Y., Ogura, T., Yudovina, Y.B., 2007. From grammatical number to exact numbers: early meanings of 'one', 'two', and 'three' in English, Russian, and Japanese. Cognitive Psychology 55 (2), 136–168.

Sasanguie, D., Defever, E., Van den Bussche, E., Reynvoet, B., 2011. The reliability of and the relation between non-symbolic numerical distance effects in comparison, same-different judgments and priming. Acta Psychologica (Amst) 136 (1), 73–80.

Sasanguie, D., Göbel, S.M., Moll, K., Smets, K., Reynvoet, B., 2013. Approximate number sense, symbolic number processing, or number-space mappings: what underlies mathematics achievement? Journal of Experimental Child Psychology 114 (3), 418–431.

Sasanguie, D., Defever, E., Maertens, B., Reynvoet, B., 2014. The approximate number system is not predictive for symbolic number processing in kindergarteners. Quarterly Journal of Experimental Psychology 67 (2), 271–280.
Sathian, K., Simon, T.J., Peterson, S., Patel, G.A., Hoffman, J.M., Grafton, S.T., 1999. Neural evidence linking visual object enumeration and attention. Journal of Cognitive Neuroscience 11 (1), 36–51.
Sekuler, R., Mierkiewicz, D., 1977. Children's judgments of numerical inequality. Child Development 48, 630–633.
Shimomura, T., Kumada, T., 2011. Spatial working memory load affects counting but not subitizing in enumeration. Attention, Perception, & Psychophysics 73 (6), 1694–1709.
Siegler, R.S., Ramani, G.B., 2008. Playing linear numerical board games promotes low-income children's numerical development. Developmental Science 11 (5), 655–661.
Smirnova, A.A., Lazareva, O.F., Zorina, Z.A., 2000. Use of number by crows: investigation by matching and oddity learning. Journal of the Experimental Analysis of Behavior 73 (2), 163–176.
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.
Sullivan, J., Barner, D., 2014. Inference and association in children's early numerical estimation. Child Development 85 (4), 1740–1755.
Toll, S.W., Van Luit, J.E., 2014. Explaining numeracy development in weak performing kindergartners. Journal of Experimental Child Psychology 124, 97–111.
Trick, L.M., Pylyshyn, Z.W., 1994. Why are small and large numbers enumerated differently? A limited-capacity preattentive stage in vision. Psychological Review 101 (1), 80–102.
Tuholski, S.W., Engle, R.W., Baylis, G.C., 2001. Individual differences in working memory capacity and enumeration. Memory & Cognition 29 (3), 484–492.
Turconi, E., Campbell, J.I., Seron, X., 2006. Numerical order and quantity processing in number comparison. Cognition 98 (3), 273–285.
Utrata, E., Virányi, Z., Range, F., 2012. Quantity discrimination in wolves (*Canis lupus*). Frontiers in Psychology 3, 505.
Van Opstal, F., Gevers, W., De Moor, W., Verguts, T., 2008. Dissecting the symbolic distance effect: comparison and priming effects in numerical and nonnumerical orders. Psychonomic Bulletin and Review 15 (2), 419–425.
Verguts, T., Fias, W., 2004. Representation of number in animals and humans: a neural model. Journal of Cognitive Neuroscience 16 (9), 1493–1504.
Verguts, T., Fias, W., Stevens, M., 2005. A model of exact small-number representation. Psychonomic Bulletin & Review 12 (1), 66–80.
Verguts, T., Van Opstal, F., 2005. Dissociation of the distance effect and size effect in one-digit numbers. Psychonomic Bulletin & Review 12 (5), 925–930.
Vetter, P., Butterworth, B., Bahrami, B., 2011. A candidate for the attentional bottleneck: set-size specific modulation of the right TPJ during attentive enumeration. Journal of Cognitive Neuroscience 23 (3), 728–736.
Vuokko, E., Niemivirta, M., Helenius, P., 2013. Cortical activation patterns during subitizing and counting. Brain Research 1497, 40–52.
Watson, D.G., Maylor, E.A., Bruce, L.A., 2007. The role of eye movements in subitizing and counting. Journal of Experimental Psychology Human Perception and Performance 33 (6), 1389–1399.
Wilson, A.J., Revkin, S.K., Cohen, D., Cohen, L., Dehaene, S., 2006. An open trial assessment of the number race: an adaptive computer game for remediation of dyscalculia. Behavioral and Brain Functions 2, 20.
Xu, F., Spelke, E.S., 2000. Large number discrimination in 6-month-old infants. Cognition 74 (1), B1–B11.
Xu, F., Spelke, E.S., Goddard, S., 2005. Number sense in human infants. Developmental Science 8 (1), 88–101.
Yaman, S., Kilian, A., von Fersen, L., Güntürkün, O., 2012. Evidence for a numerosity category that is based on abstract qualities of "few" vs. "many" in the bottlenose dolphin (*Tursiops truncatus*). Frontiers in Psychology 3, 473.