

Behavioral and Neural Basis of Number Sense in Infancy

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ABSTRACT—Approximate number discrimination in adult human and nonhuman animals is governed by Weber's Law: The ratio between the values determines discriminability. Here, we review recent evidence from behavioral and neuroimaging studies that suggests that number sense in human infancy shares the same hallmark feature of Weber's Law and may rely on the same neural substrates as previously found in adults, children, and nonhuman animals. These findings support the notion of ontogenetic and phylogenetic continuity in number sense. New methods described here may help uncover how infants' early number sense supports the development of a mature number sense. Moreover, they may aid in understanding how children learn to map nonsymbolic number representations onto symbols for number by providing dependent measures that capture individual variability.

KEYWORDS—numerical cognition; number sense; cognitive development; Weber's Law; intraparietal sulcus

Numbers are ubiquitous in our everyday life. As educated adults we use a variety of different formats to keep track of numbers, such as spoken or written number words, Arabic or Roman numerals, or tallies. However, there are many everyday situations in which we approximate instead of determining the exact number (e.g., when comparing two checkout lines at the store). This paper will exclusively focus on this latter type of approximate number representation that enables us to represent and manipulate numerical quantities nonsymbolically—that is, without applying labels such as number words—and that is also referred to as *number sense* (see, e.g., Dehaene, 1997, for a review). In particular, we review current advances and directions in our understanding of the development of approximate number sense during infancy and the nature of its neural underpinnings. These advances provide critical groundwork for future research

exploring the relationship between early number sense and later math abilities.

ONTOGENETIC CHANGES IN NUMBER SENSE

A wealth of behavioral studies has shown that infants are capable of discriminating sets of objects based on the number of elements in each set. Here, we exclusively focus on infants' abilities to discriminate large numbers (i.e., numbers greater than 3). Using variants of the standard visual habituation paradigm widely employed in developmental psychology and carefully controlling for non-numerical aspects of the stimuli that could be confounded with number, Spelke and colleagues (e.g., Lipton & Spelke, 2003; Xu & Spelke, 2000) have shown that 6-month-old infants can discriminate an array of, for instance, 8 dots or sequences of sounds from an array or a sequence of 16 (1:2 ratio), but fail to discriminate 8 from 12 (2:3 ratio). At 9 months, infants are able to discriminate 8 from 12 but fail to discriminate 8 from 10 (4:5 ratio; Lipton & Spelke, 2003). These ratio limits have been found to hold for numerical discrimination both in the visual as well as the auditory domain, suggesting that the number-discrimination process operates on a representation that is independent of input modality and that it is indeed numerical discrimination that improves with age and not just with increasing perceptual discrimination abilities.

A recent study shows that, even beyond infancy, numerical discrimination continues to improve with age. Halberda and Feigenson (2008) tested children and adults on a nonverbal number-comparison task and found marked improvement between 3 and 6 years of age—from a 3:4 ratio to a 5:6 ratio, respectively. Importantly, even the oldest age group in their sample had not yet reached adult levels of discrimination, which in this case was as high as a 10:11 ratio. Thus, number sense seems to develop and improve well into childhood even after formal mathematics instruction commences. These findings leave open the question of how such nonverbal numerical acuity relates to more symbolically mediated mathematical skills.

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NEURAL LOCUS OF NUMBER SENSE ACROSS THE LIFE SPAN

Neuroimaging research with adults suggests that the intraparietal sulcus (IPS; Fig. 1)—a posterior parietal brain region—represents approximate numerical information regardless of whether it is presented symbolically or nonsymbolically and regardless of whether the information is presented visually or auditorily (see, e.g., Dehaene, Molko, Cohen, & Wilson, 2004, for a review). Similar research with children has shown that activation in the IPS in nonsymbolic number processing is present in children as young as 4 years of age and parallels that found in adults in the same study (Cantlon, Brannon, Carter, & Pelphrey, 2006; Temple & Posner, 1998) but that its involvement increases with age (Ansari & Dhital, 2006; Cantlon et al., in press). Despite the large number of studies that have examined the neural underpinnings of number representations in adults and the growing number of studies in children, only very few studies have investigated the neural correlates of numerical cognition in infancy.

Using a numerical violation-of-expectation paradigm in combination with event-related potentials (ERPs), Berger and colleagues (2006) investigated infants' neural response when viewing events that could be interpreted as arithmetically correct or erroneous operations within the small number range. In this paradigm, infants were presented with movies in which one or two toys were placed on a stage and subsequently occluded by a screen. In the Addition condition, the infant watched as a

second toy was placed behind the screen, and in the Subtraction condition, the infant observed as one of two occluded toys was removed from behind the screen. After the addition or subtraction event the screen was lowered to reveal either the correct number of toys or an incorrect number (e.g., only one toy in the Addition condition or two toys in the Subtraction condition). Analyses of the electrical activity along the scalp in response to the outcome of the arithmetic manipulations showed significant differences in brain activity over frontal and central scalp sites for the incorrect versus the correct arithmetic solution. Moreover, further analyses suggest that the magnitude of theta ($\sim 4\text{--}8$ Hz) and alpha ($\sim 8\text{--}12$ Hz) oscillations in the brain activity time-locked to the presentation of the solution was greater for the incorrect as compared to the correct arithmetic solution over similar brain regions. A similar pattern of ERP and oscillatory results was found in adults tested in a symbolic arithmetic error-detection task. These findings suggest that infants may employ an error-detection mechanism that is similar in nature to adults' arithmetic error-detection mechanism and do not support the idea that infants' performance is due solely to the understanding that objects continue to exist even when they cannot be directly perceived (e.g., Simon, 1997). However, this study is not explicitly concerned with the neural basis of the underlying numerical representation and cannot elucidate whether the observed effects are specific to arithmetic or a more general error-detection response. Furthermore, the study employed exclusively small values with infants and thus may not have tapped an approximate number sense.

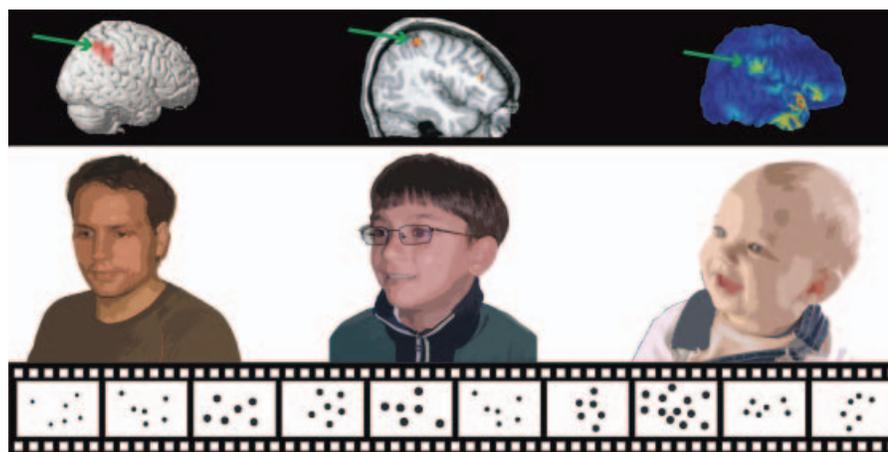


Fig. 1. Passive nonverbal numerical adaptation paradigm (bottom row) and brain-activation findings for adults (left), 4-year-old children (middle), and infants (right). All three age groups show changes in brain activation in or near the intraparietal sulcus (green arrows) when an infrequent numerical stimulus (bottom, third frame from right) deviates from the frequently presented numerosity. Left brain image reproduced from “Tuning Curves for Approximate Numerosity in the Human Intraparietal Sulcus,” by M. Piazza, V. Izard, P. Pinel, D. Le Bihan, & S. Dehaene, 2004, *Neuron*, 44, 547–555. Copyright 2004, Elsevier. Reproduced with permission. Middle brain image reproduced from “Functional Imaging of Numerical Processing in Adults and 4-y-Old Children,” by J.F. Cantlon, E.M. Brannon, E.J. Carter, & K.A. Pelphrey, 2006, *PLoS Biology*, 4, e125. Copyright 2006, Public Library of Science. Reproduced with permission. Right brain image reproduced from “Distinct Cerebral Pathways for Object Identity and Number in Human Infants,” by V. Izard, G. Dehaene-Lambertz, & S. Dehaene, 2008, *PLoS Biology*, 6, e11. Copyright 2008, Public Library of Science. Reproduced with permission.

In another ERP paradigm, Izard, Dehaene-Lambertz, and Dehaene (2008) tested 3-month-old infants in a visual adaptation paradigm in which infants were repeatedly shown arrays of, for example, four yellow cartoon animals, in order to adapt them to both the number and the identity of the objects. Occasional test images contained either a novel number of the same cartoon animals, the same number of items but a novel animal shape, or both a novel number and novel animal shape. Number changes but not identity changes elicited large ERP differences over right parietal (dorsal visual pathway) scalp sites, whereas identity changes but not number changes elicited differences over occipito-temporal (ventral visual pathway) areas. These findings suggest an early differentiation of processing pathways for numbers versus objects and also indicate that, already at 3 months of age, parietal areas may contribute to numerical information processing (Fig. 1).

PARALLELS BETWEEN INFANTS' AND ADULTS' NUMBER SENSE

When comparing relative values, a consistent finding with human adults, children, and nonhuman animals across a variety of different nonsymbolic and symbolic numerical notations (e.g., visual or auditory, as symbols or sets of objects) is that the larger the numerical disparity (e.g., 6 vs. 12 compared to 6 vs. 8), the faster and more accurate the judgment—a phenomenon known as the distance effect. Moreover, when numerical distance is held constant (e.g., 6 vs. 8 compared to 12 vs. 14), accuracy decreases and response times increase for larger magnitudes, a phenomenon known as the size effect. The distance and size effects together yield Weber's Law: The ratio between quantities determines their discriminability.

An explanation for the occurrence of Weber's Law in number discrimination is that numerical information is represented as inexact mental magnitudes on a mental number line (e.g., left to right in psychological space) with peaks centered approximately on the number to be represented. As numbers get larger, either the error in the representation increases (Gibbon, 1977) or the peak values become closer to each other on the mental number line, rendering numbers that are more distant from each other numerically more distinguishable (Dehaene, 1997). Weber's Law is observed in a variety of perceptual domains (e.g., brightness, weight, time) suggesting that other non-numerical magnitudes may be represented in a similar way.

The fact that Weber's Law guides number discrimination in human adults, children, and nonhuman animals suggests an ontogenetic and phylogenetic continuity in number sense. However, due to methodological limitations, prior studies have not provided definitive evidence for Weber's Law in infancy. As reviewed above, infants' success at discriminating numbers seems to be determined by the ratio between the numerical values. However, this finding falls short of the vast psychophysical literature in human adults, older children, and non-

human animals that shows that discrimination even across a broad range of discriminable values is ratio dependent. In contrast, the standard experimental paradigms used to test infants, which are based on binary success or failure patterns, have found that infants require a minimum ratio for discrimination, but these paradigms have not been able to determine whether ratio dependency holds for a wider range of values beyond this minimum ratio. Our lab recently designed two novel paradigms to address this question directly.

We first used EEG to investigate whether there are neural markers in infancy that reflect ratio-dependent number discrimination (Libertus, Pruitt, Woldorff, & Brannon, in press). We asked whether number-sensitive neural responses vary as the discriminability between numerosities increases. In that study, we recorded EEG while 7-month-old infants were first familiarized to a given numerosity and later presented with novel images of the familiar numerosity (1:1 ratio) and novel images of either one or two novel numerosities. Novel numerosities differed by a 1:2 or a 1:3 ratio from the familiar numerosity. We found that alpha-band (6–8 Hz) and theta-band (4–6 Hz) oscillations both differed for novel and familiar numerical values. Most importantly, however, spectral power in the alpha band over midline and right posterior scalp sites was modulated by the ratio between the familiar and novel numerosities—the larger the relative difference between numerosities (1:3, 1:2, vs. 1:1 ratio), the smaller the power in the alpha-frequency range (Fig. 2a). No differences were found in alpha power between numerical values that both differed by a 1:2 ratio but employed different numerical values. The finding that alpha-band power changes as a function of numerical ratio independent of absolute differences between numerical values is strong evidence that numerical discrimination in infancy is ratio dependent. Furthermore, it is noteworthy that no such pattern was observed in the ERP analysis, suggesting that analyses of induced frequency changes in the EEG may be able to extract information otherwise lost in standard ERP analyses that rely on consistently time-locked neural responses.

The second paradigm is a behavioral numerical change detection method in which infants are presented with two image streams simultaneously on two peripheral monitors (Libertus & Brannon, in press). One of the streams is numerically constant (but perceptually changing) and the other alternates between two numerosities. Using this paradigm, we found that 6-month-old infants preferred to look at the numerically changing stream when the two values differed by a 1:4, 1:3, or 1:2 ratio but did not show any differential preference when the two values in the numerically changing stream differed only by a 2:3 ratio (Fig. 2b). Most importantly, we found a significant linear increase in preference for the numerically changing stream over the other stream as numerical disparity between the two values in the changing stream increased from a 1:2 to a 1:4 ratio. Furthermore, there was no difference in preference scores between two conditions that both differed by a 1:2 ratio but used different absolute values (i.e., 10 vs. 20 and 8 vs. 16). While these results

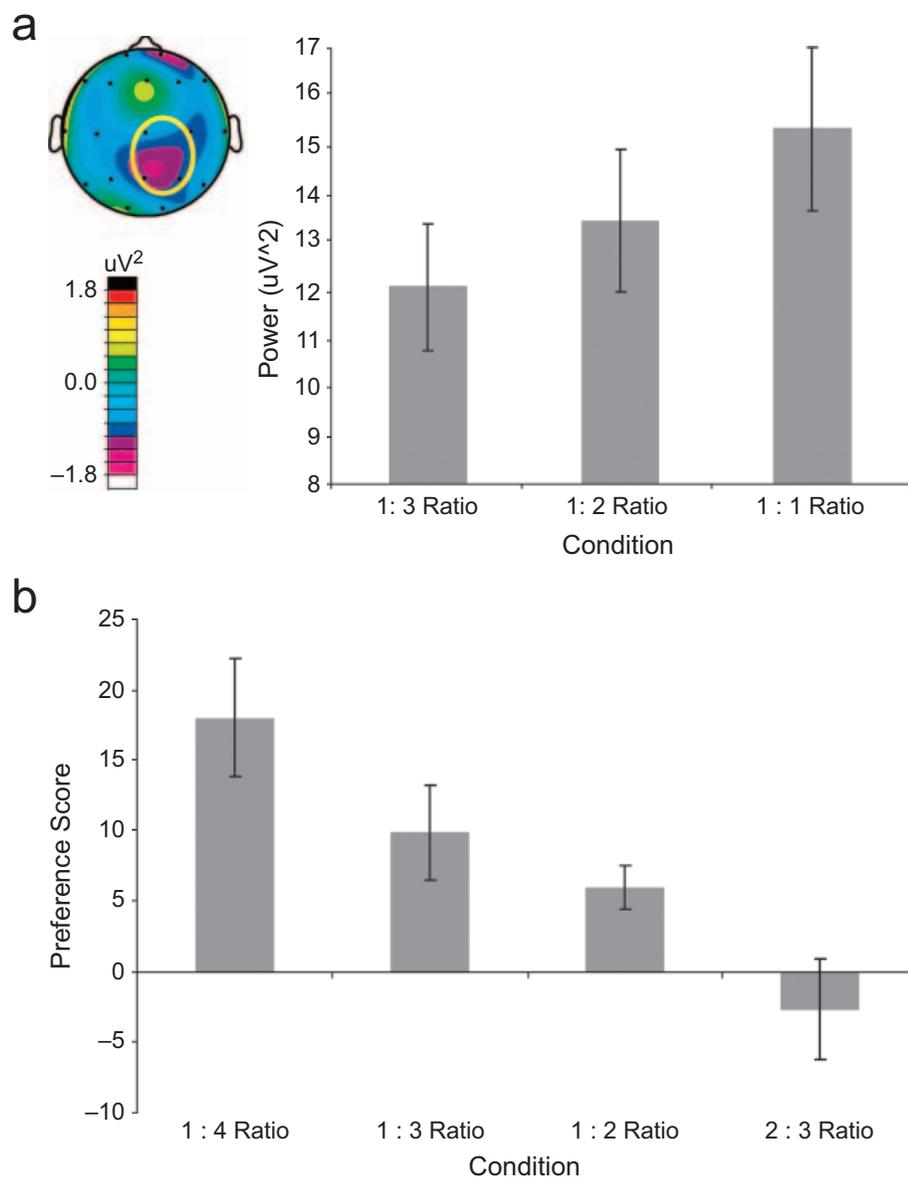


Fig. 2. Evidence for ratio-dependent number discrimination in infancy provided by two separate studies. (a) Power in the 6 to 8 Hz alpha-frequency band of the infant electroencephalogram (EEG) decreases as a function of numerical ratio between a familiar and novel numerosity (1:3, 1:2, or 1:1). Effects of numerical novelty and ratio dependency in the alpha-band were found over parietal and central scalp sites (see insert in Fig. 2a). (b) Infants' preference to look to a numerically changing image stream as compared to a numerically nonchanging image stream increases as a function of numerical ratio. Panel (a) reproduced from "Induced Alpha-Band Oscillations Reflect Ratio-Dependent Number Discrimination in the Infant Brain," by M.E. Libertus, L.B. Pruitt, M.G. Woldorff, & E.M. Brannon, in press, *Journal of Cognitive Neuroscience*. Reproduced with permission. Panel (b) reproduced from "Stable Individual Differences in Number Discrimination in Infancy," by M.E. Libertus & E.M. Brannon, in press, *Developmental Science*. Reproduced with permission.

replicate previous findings using other behavioral paradigms, they provide more definitive evidence that infants' number discrimination is governed by Weber's Law, because the strength of the effect changes with the ratio between the two values in the numerically changing stream.

An important question for the field of cognitive development is the nature of the relationship between infants' knowledge as

assessed by looking-time measures and later childhood knowledge. The behavioral change detection paradigm described above may hold promise for elucidating this relationship in the domain of number. While the ratio-dependent effects described above are derived from between-subject analyses, follow-up testing of a subset of these infants suggests that individual differences in infants' preference scores in the numerical change

detection task are reliable between 6 and 9 months of age. We plan to use this procedure to track individual differences in numerical sensitivity from infancy into early and later childhood. Such data would provide insight into the role of infant number sense in the development of a mature number sense. A recent study by Halberda and colleagues (2008) found that nonverbal numerical acuity in adolescence was a significant predictor of performance on standardized math tests in kindergarten. An important next step is to determine whether infants' nonverbal acuity predicts later math abilities.

CONCLUSIONS AND FUTURE DIRECTIONS

Recent neuroimaging and behavioral studies reveal important parallels between both the neural basis and behavioral signatures of number discrimination in infancy and adulthood. Specifically, behavioral and electrophysiological studies indicate that the ratio between numerosities not only determines infants' success or failure to discriminate, but that Weber's Law governs numerical comparison even for values above the threshold for numerical discrimination. These parallels suggest that infants possess the same analog magnitude system as adults, older children, and nonhuman animals.

We are hopeful that new methods will shed light on the important question of how the infantile number sense is related to the mature number sense. One possibility is that early number sense is foundational and provides the conceptual basis for mapping numerical symbols onto their meaning (e.g., Dehaene, 2001; Gelman & Butterworth, 2005). An alternative idea is that the analog magnitude system is peripheral as children learn to verbally count and perform symbolic arithmetic and only later do children map analog magnitudes onto number words and symbols (e.g., Carey, 2001). By developing methods like the numerical change-detection paradigm that produce meaningful dependent measures for individual subjects, we can begin to track the relationship between infants' number sense and later-emerging abilities. Novel paradigms such as the change-detection paradigm might provide the necessary tools to assess number sense across infancy and later childhood to further our understanding of the development of numerical representations, the functional role of number sense, and its relation to exact representations of number. These tools may also be valuable to gain insights into math deficits (see Rubinsten & Henik, 2009, for possible explanations). More generally, developmental studies provide a unique opportunity to delineate the causal link between early number sense and symbolic number systems as children's mathematical minds develop.

Recommended Reading

Carey, S. (2009). *The origin of concepts*. New York: Oxford University Press. A book providing a detailed discussion about conceptual development beyond numerical cognition.

- Cordes, S., & Brannon, E.M. (2008). Quantitative competencies in infancy. *Developmental Science*, *11*, 803–808. A review of evidence of two separate systems for representing small and large numbers in infancy and discusses the similarities and differences in infants' abilities to discriminate discrete and continuous quantities.
- Dehaene, S. (1992). Varieties of numerical abilities. *Cognition*, *44*, 1–42. An in-depth introduction to numerical cognition and the triple-code model of number representation.
- Gallistel, C.R., & Gelman, R. (2005). Mathematical Cognition. In K.J. Holyoak & R.G. Morrison (Eds.), *The Cambridge handbook of thinking and reasoning* (pp. 559–588). New York: Cambridge University Press. Book chapter providing a detailed review of the approximate number system and its relationship to verbal and written number systems.
- Halberda, J., Mazocco, M.M., & Feigenson, L. (2008). (See References). Longitudinal study showing that there are large individual differences in number sense even at 14 years of age, and that these individual differences in the present correlate with children's past scores on standardized math achievement tests, extending back to kindergarten.

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