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Neuroscientist 2009; 15; 261

DOI: 10.1177/1073858409333073

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The Neuroscientist
Volume 15 Number 3
June 2009 261-273
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10.1177/1073858409333073
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Numerosity (the number of objects in a set), like color or movement, is a basic property of the environment. Animal and human brains have been endowed by evolution by mechanisms based on parietal circuitry for representing numerosity in an highly abstract, although approximate fashion. These mechanisms are functional at a very early age in humans and spontaneously deployed in the wild by animals of different species. The recent years have witnessed terrific advances in unveiling the neural code(s) underlying numerosity representations and showing similarities as well as differences across

species. In humans, during development, with the introduction of symbols for numbers and the implementation of the counting routines, the parietal system undergoes profound (yet still largely mysterious) modifications, such that the neural machinery previously evolved to represent approximate numerosity gets partially “recycled” to support the representation of exact number.

Keywords: parietal lobe; number processing; fMRI; electrophysiology; macaque monkey; evolution

Numerosity, the cardinality of a set, is a property that applies to any set of individual objects. It is abstract in the sense that it does not depend on the nature of the items themselves (“five” may well apply to the fingers of a hand, tones in a melody, as well as to abstract entities like ideas or personality traits). Human and nonhuman animals’ brains have been endowed by evolution with a set of mechanisms to extract and internally manipulate numerosity at a quite abstract level. Such mechanisms are functional at a very early age in humans and spontaneously deployed in the wild by animals of different species. Indeed, being able to perform number-based judgments has a clear strong ecological value: it is crucial for foraging, social interactions, and sometimes even for planning reproductive strategies. In humans, the ability of accessing numerosity in a nonverbal nonsymbolic way, shared with nonhuman animals, coexists with the ability to assess exact large cardinal values, an operation that involves complex counting routines that children take long to master, adults in different cultures perform in quite different ways, and populations in some remote cultures can lack altogether.

In this article, first we will describe the cognitive and neural mechanisms underlying the approximate quantification system that we humans share with

animals, and then we will describe the cognitive and neural underpinnings of the exact quantification systems, including the operations of counting, used by humans to get exact representations of large cardinal values. Throughout the manuscript, although we will mainly focus on humans, we will always integrate both behavioral and neural data from the nonhuman animal literature in the attempt to keep a clear evolutionary perspective and to have an integrated view from different methodologies.

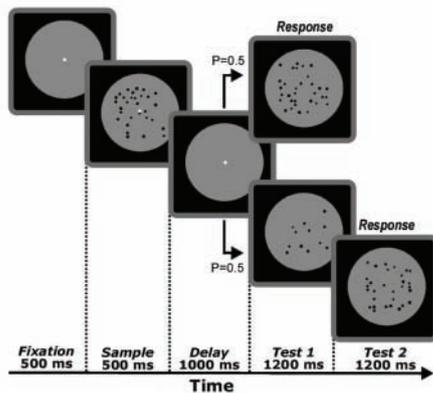
Approximate Representations of Numerosity

When human adults discriminate or compare the number of pairs of arrays or sequences of items under conditions that prevent counting, responses are approximate and become increasingly accurate as the difference between the numbers increases, in a way that is solely modulated by their ratio. This ratio-dependent behavior is an instance of Weber’s law, which is typically found in judgments of continuous perceptual variables such as length, luminance, or frequency. Weber’s law is very pervasive in numerical cognition: it is observed in human adults living in occidental or remote cultures, in children, infants, and also in various animal species, performing many different tasks, from simple comparison to more challenging arithmetical operations (Piazza and others 2004; Pica and others 2004; Cantlon and Brannon 2007), or estimation (Cordes and others 2001; Izard and Dehaene 2008) (see Fig. 1B for an example of Weber law in monkey behavior, and Fig. 2B for similar evidence in humans). In the latter case,

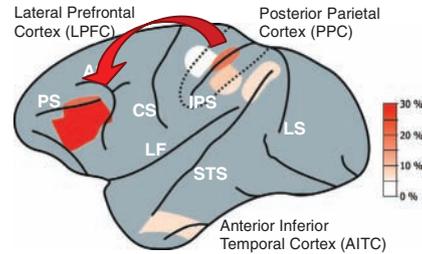
From the Center for Mind/Brain Sciences, University of Trento, Italy (MP); Dipartimento di Scienze della Cognizione e della Formazione, Università di Trento, Italy (MP); INSERM, U562, Cognitive Neuroimaging Unit, Gif/Yvette, France (MP); and Department of Psychology, Harvard University, Cambridge, Massachusetts (VI).

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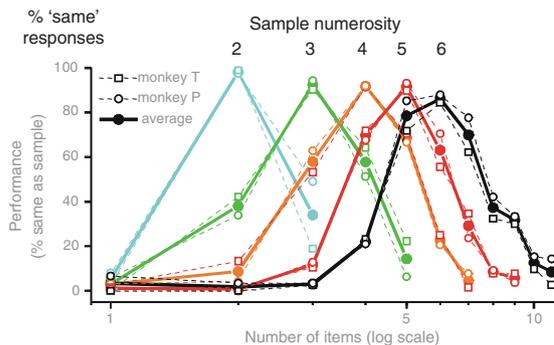
A. Numerosity match-to-sample protocol



C. Recording sites (% of number selective neuron)



B. Behavioral discrimination (% 'same' responses)



D. VIP Neuronal tuning functions

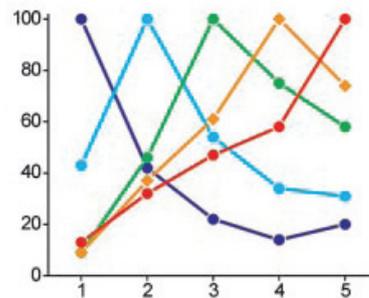


Figure 1. Numerosity-selective neurons in the monkey intraparietal sulcus and lateral prefrontal cortex. A, Example of delayed match-to-sample task: Monkeys were cued for a given numerosity (here ranging from 1 to 30) by a sample display. They had to memorize the numerosity in a 1-second delay period and match it to a subsequent test stimulus by releasing a lever (from Nieder and Merten 2007). In another set of experiments (Nieder and Miller 2003), sample stimuli ranged from 1 to 6. B, The behavioral performance of two monkeys indicated whether they judged the first test stimulus (after the delay) as containing the same number of items as the sample display (“% same as sample”). Colors represent performance curves for a given sample numerosity (from Nieder and Miller 2003). C, Location of recording sites. Lateral view of a monkey brain showing the recording sites in the prefrontal and parietal cortex. The proportions of numerosity-selective neurons in each area are color coded. The arrow indicates the presumed direction of information flow, derived from the firing onset of number neurons in the two regions (from Nieder and Miller 2004). D, Response properties of numerosity-selective neurons in the parietal cortex in terms of normalized average activity (from Nieder and Miller 2004).

the ratio dependence is instantiated by scalar variability in the responses: the trial-by-trial variability of the estimates increases proportionally to the estimate. The universality of Weber’s law in animals, humans of all age, and education is taken to indicate the presence of a universal mechanism for approximate number processing.

The Neural Codes for Approximate Representations of Numerosity in the Human and Animal Brain

Since the pioneer study of Thompson and colleagues (Thompson and others 1970), it is known that the posterior associative cortex of the cat (possibly homologous to primates’ posterior parietal cortex) contains

neurons that code for numerosity. This initial discovery was recently confirmed by two groups working in the awake macaque monkey (Nieder and others 2002; Sawamura and others 2002). One group trained animals to perform a different number of movements in sequence and showed that neurons in the anterior bank of the intraparietal sulcus responded selectively to the numerical information (i.e., the position of the movement in the sequence), independent from the timing and the type of movement (Sawamura and others 2002). Those neurons were responding maximally to a preferred value, but their tuning functions—that is, the average responses plotted in function of numerosity—were quite broad, suggesting an approximate coding. The other group used a numerosity match-to-sample task on visual sets of items, and showed that neurons

in the depth of the intraparietal sulcus, in a region later functionally defined as VIP (see below), fired preferentially for a given number even across a broad variation of stimuli that controlled for object size, density, spacing, and spatial layout (Nieder and others 2002; Nieder and Miller 2003). Although similar neurons were also found in the prefrontal cortex, the analysis of the neurons' response latencies suggested that parietal neurons first extract the numerosity information and then project it to PFC neurons, which would be involved in the online maintenance of the information for the delayed match-to-sample task (Nieder and Miller 2003). This study also reported a detailed analysis of the tuning functions of these neurons, revealing that they obey Weber's law: The width of the tuning curves increases linearly with the numerosity encoded, in tight agreement with the distribution of behavioral responses (compare Fig. 1B and 1D).

The monkey intraparietal code for numerosity might be the evolutionary precursor for the human ability to extract and internally manipulate numerical quantity. Indeed, the relevance of the parietal cortex in number-related tasks has been known since the work of the German neurologist Henschen who was the first one to link the impairments in number processing to the parietal cortex. More recently, several neuroimaging studies in humans showed that a specific portion of the parietal cortex, namely, the horizontal segment of the intraparietal sulcus (hIPS), is consistently activated whenever adults from different countries and cultures compute simple comparison, or perform calculation on symbolic notations such as Arabic numerals or number words (Dehaene and others 2003). Based on these observations, and on the fact that the activation in the hIPS increases as the task puts greater emphasis on quantity processing, we proposed that the hIPS might be the locus of a core system for representing numerical quantity, and thus that it should be also crucial for the manipulation of numerosities (Dehaene and others 2003). Important evidence in favor of this hypothesis was to come one year later, when using fMRI-adaptation we revealed, in the human intraparietal sulcus, the putative homologous of the previously individuated numerosity-selective neurons in the intraparietal sulcus of the macaque monkey (Piazza and others 2004). During fMRI, we repeatedly presented sets of a fixed number of dots (for example, 16 dots) to "adapt" the neural population coding for this value, leading such putative neural population to progressively reduce their firing rate. We then presented occasional deviant numbers that ranged from half to twice the adapted number. fMRI revealed that only two regions, the left and right hIPS, responded to the changes in numerosity by increasing their activation in relation to the ratio between the adapted number and the deviant one, regardless of the direction of the change (more or fewer dots).

Analysis of the distribution of the response to different deviant stimuli showed that the size of the rebound effect was solely modulated by the ratio between the deviant and the adaptation numerosity, in excellent agreement with Weber's law (see Fig. 2).

That numerosity processing activates the hIPS region in humans has now been replicated several times using different stimuli such as sequences of sounds versus patterns of dots, serial versus simultaneous presentation of visual stimuli, and different paradigms such as passive viewing versus active computations (Piazza and others 2004; Piazza and others 2006). Using the same fMRI adaptation paradigm as in Piazza and others, Cantlon and colleagues tested four-year-old children and confirmed the hypothesis that the parietal mechanism of numerosity extraction is already functional early in life, and prior to arithmetical education (Cantlon and others 2006). Recently we applied the adaptation paradigm to three-month-old infants, using EEG (Izard and others 2008a). The recordings showed a specific response to numerosity changes in the infant brain, originated from a fronto-parietal network, which differed from the response observed for a change in shape (see Fig. 3). This network could reflect an early bias for numerical information to be processed within the dorsal stream, later giving rise to the development of number-sensitive areas in the hIPS (Fig. 3).

Final evidence for the causal role of the hIPS in numerosity processing comes from "virtual lesions" TMS studies that show, for example, that rTMS over the hIPS, and not Angular Gyrus, disrupt numerosity judgments, and that numerosity, and not duration processing, is affected by rTMS over the hIPS (Cappelletti and others 2007; Dormal and others 2008).

In sum, several labs now have collected converging evidence for the existence of an early active numerosity detector system that represents number in a continuous, approximate, and compressed fashion, according to the principles of Weber's law. This system is likely to be evolutionary ancient and shared across species.

Homologies of the Parietal Code for Numerosity across Species

The similarity between the code for number as indirectly measured by fMRI in humans and the tuning profiles of the numerosity coding neurons in the macaque monkeys is indeed striking. The question is whether the regions containing number neurons are indeed homologous across species. In monkeys, cytoarchitectonic, connectivity, and physiological data suggest that the IPS is functionally segregated into subregions that, following a posterior-to-anterior gradient, code for space in either eye (LIP), head (VIP), or hand-centered (AIP) frames of reference (see Hubbard and others 2005 for a review). Number neurons were tentatively localized in the medial

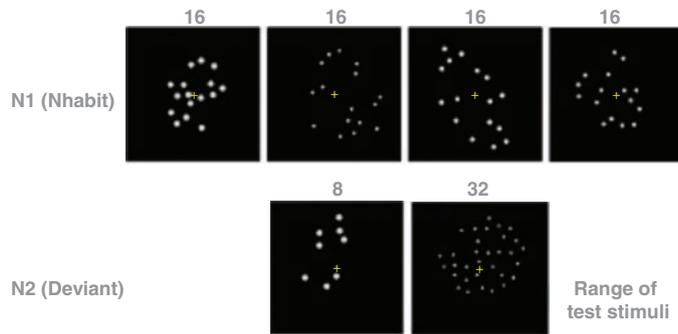
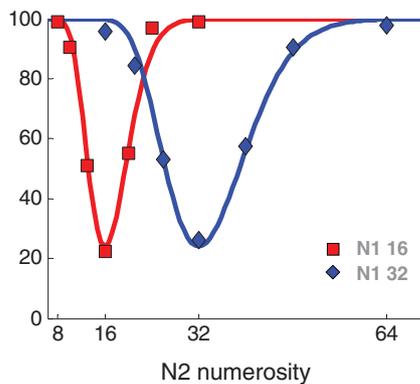
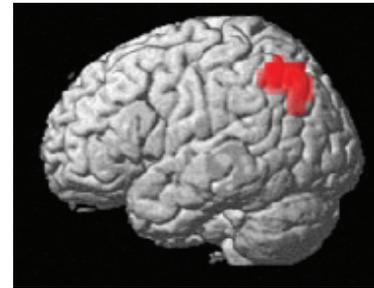
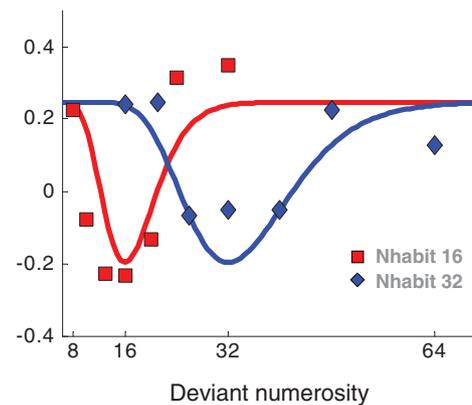
A. Numerosity adaptation protocol**B. Same-Different Task (% “different” responses)****C. Response to change in numerosity****D. Parietal cortex activation**

Figure 2. Numerosity-related responses in the human intraparietal sulcus. A, Participants were presented with a stream of visual arrays of constant numerosity (here illustrated with 16), which varied in terms of all other nonnumerical parameters (size of the dots, total summed area, density, total occupied surface). Occasional numerical changes (deviants) were inserted in the stream, which could depart from the adaptation numerosity in either direction (smaller or larger), and with different values of ratio (max 2.0; in the illustrated example, the range of variation was therefore 8–32). B, The same stimuli were used in a same-different task with references 16 and 32, and judgments depended on the ratio between numerosities. C, Left parietal responses to changes in numerosity. D, Activation to the different deviant sets is plotted as a function of the adaptation numerosity. In red, adaptation value as equal to 16, in blue, 32 (Piazza and others 2004).

region VIP (Tudusciuc and Nieder 2007), a region containing multisensory neurons coding for different combinations of visual, vestibular, somatosensory, and auditory stimuli, mainly aligned to the head (Sereno and Huang 2006). Number-selective neurons were shown to respond to both visual flow-field stimuli and tactile stimuli over the monkey’s head, typical of VIP.

In humans, fMRI studies have used tasks inspired by monkey physiology to identify putative homologues of the macaque IPS regions, and have confirmed the posterior-to-anterior organization. In particular, the human VIP (hVIP) responds to somatosensory, visual, and auditory stimuli, and contains aligned head-centered visual and tactile maps, thus sharing crucial functional properties with the macaque monkey VIP (Bremmer and others 2001; Sereno and Huang 2006). Interestingly, Hubbard

and colleagues recently identified hVIP by means of a conjunction between the activation to flow-field stimuli and to tactile stimulation of the face, and reported the peak coordinates at voxels remarkably close to the ones showing numerosity adaptation effects (Piazza and others 2004; Hubbard and others 2008).

Is the Internal Representation of Number Abstract?

One important question is to what extent the numerosity representation is abstract. Behaviorally, identical Weber’s law signatures are found when subjects (human adults, children, animals) compare or match the number of stimuli presented in different modalities (auditory, visual) and in different modes (sequentially or

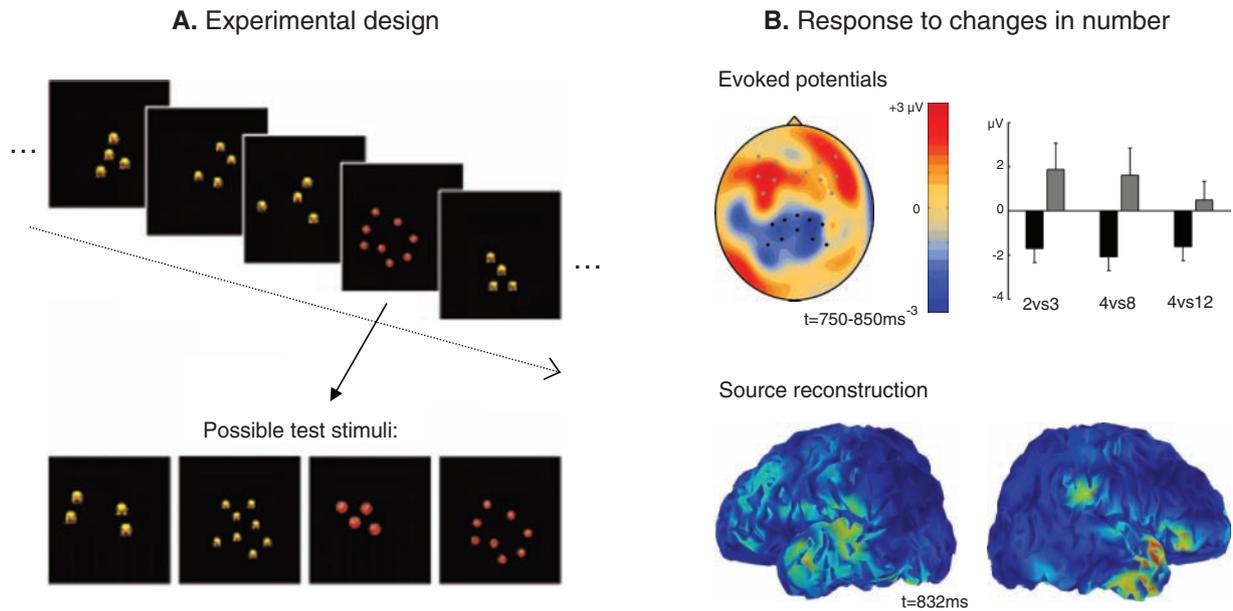


Figure 3. Cerebral response to changes in numerosity in infants. A, Three-month-old infants were presented with a stream of visual arrays, with occasional numerosity deviant stimuli. B, Changes in numerosity elicited a brain response around 800 ms after the presentation of the stimulus. The response consisted of a bilateral parietal negativity, coupled with positive voltages over anterior electrodes and was present in three groups of infants, irrespective of the size of the numerosities presented. Source localization linked this response to activity in a right parieto-prefrontal network (specific to changes in number) and in the temporal lobe (also present for changes of object).

simultaneously) (Cordes and others 2001; Hauser and others 2003; Piazza and others 2004). Similarly, the activation of the hIPS remains unchanged across major changes in the stimulus modality (visual and auditory) or mode (sequential or simultaneous) (Piazza and others 2004; Piazza and others 2006).

Most important, subjects can match and manipulate numbers *across* senses (e.g., across auditory and visual stimuli, for example), and they do so without additional costs with respect to within senses (Barth and others 2005). For animals and preverbal infants, however, the evidence is mixed, as positive cross-modal matching has only been observed in the small number range, where subjects could be responding based on a one-to-one correspondence between elements across senses (Jordan and others 2008). In the large number range, the evidence for abstract numerical representations reported so far is only suggestive, but recent results obtained in our lab confirmed that infants can match large numbers across the auditory and visual modalities (Izard and others 2008b). Another piece of evidence that language is not responsible for the development of an abstract code for numerosity comes from speakers of Piraha, a language with no known numeric lexicon (Gordon 2004; Frank and others 2008). Participants were asked to reproduce the number of items in arrays presented in various formats. Even when the format of the target array and the response array differed maximally, the numerosity estimates showed the characteristic signature of scalar variability (see above).

Electrophysiological recordings in animals have further clarified the extent to which numerosity is coded in an abstract fashion. Indeed, the very first report of numerosity coding neurons in the posterior associative cortex of cats showed identical response to a given number irrespective of stimuli modality (visual and auditory) (Thompson and others 1970). Number neurons later localized in the macaque monkeys' parietal cortex (across studies) for the number of motor sequences performed (Sawamura and others 2002) and of objects presented in visual arrays (Nieder and others 2002). Finally, recordings in the same monkeys with the same experimental paradigms showed that, at least in some number neurons, the code is abstract enough to respond to both sequential and simultaneous presentations of number (Nieder and others 2006).

The Weber Fraction and Its Development

Although abstract to the point described above, the internal representation of numerosity obeys the same laws that govern judgments of continuous perceptual variables such as length, luminance, or frequency. Because of this, numerosity is thought to be internally represented in a quantitative analogous format, an idea captured by the metaphor of the mental number line. However, the question of the scaling of the number line remains debated. On one hand, Dehaene proposed that the number line is logarithmically compressed, with a fixed internal variability (Dehaene and Changeux 1993).

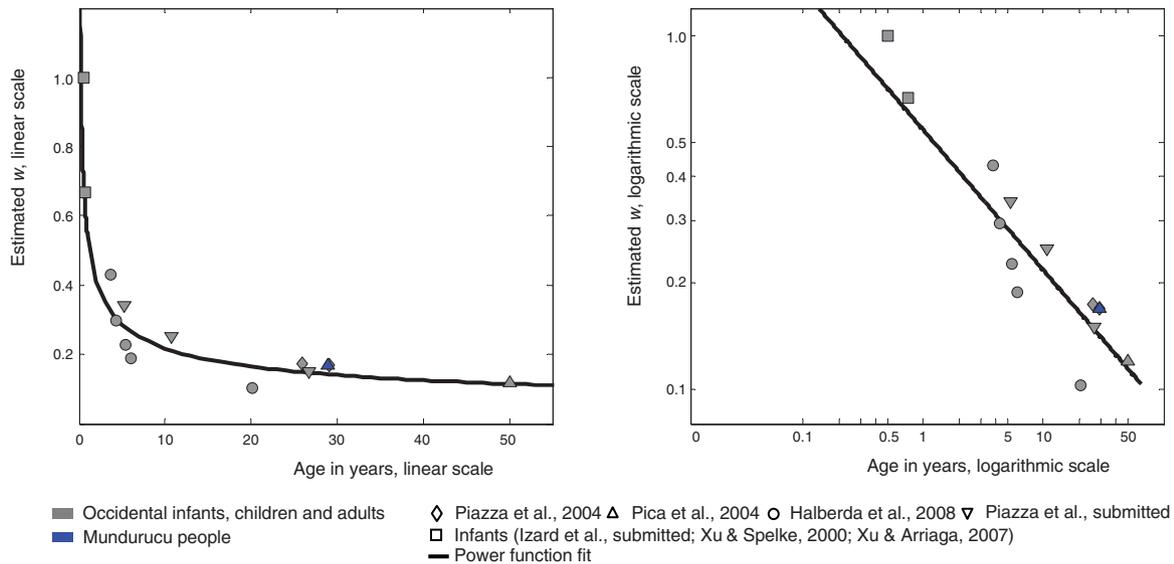


Figure 4. Development of the precision of the approximate numerical representations. The graphs regroup the values of w estimated in different papers (diamonds: Piazza and others 2004; upward triangle: Pica and others 2004; circle: Halberda and Feigenson 2008; downward triangle: Piazza and others 2008; square: infant data from Xu and Spelke 2000 and Xu and Arriaga 2007). The developmental trend is well fitted by a power function of exponent -0.40 (solid line) ($R^2 = 0.70$). Mundurucu people from the Amazon are represented in blue and do not depart from the trend observed in occidental subjects.

Such scale ensures that the amount of overlap between two numbers depends on their ratio, predicting Weber's law on behavior. Alternatively, numerosities could be internally coded on a linear scale with proportionally increasing standard deviation of the internal noise, thus also predicting Weber law on behavior (Gallistel and Gelman 2000).

In an attempt to resolve this issue, Nieder and colleagues (Nieder and Miller 2003) examined monkey behavior (and neural firing) in a match-to-sample task, where response distributions around the sample's (preferred) numerosity are asymmetrically skewed toward large values and become symmetrical when plotted on a logarithmic scale. This last property is taken as supporting the logarithmic scaling model. However, symmetry on a logarithmic scale reflects nothing more than Weber's law: On a log scale, the two numbers situated on either side of the sample numerosity differ from this center numerosity by the same ratio; thus Weber's law predicts that their response curves should be symmetric on a logarithmic scale. Because both linear and logarithmic number line models predict that Weber law, asymmetries cannot be taken as favoring one or the other.

Both models introduce the same parameter to measure the global precision of the number representations, called "internal Weber fraction" (w). This measure corresponds to the standard deviation of the estimated Gaussian distribution of the internal representation of numerosity that generates the observed performance (an idea previously described in the Supplemental Data

from Piazza and others 2004, and further elaborated in Dehaene 2007). Thus, $2w$ represents the percentage difference between two numerosities that is necessary to perceive them as different with $\sim 95\%$ confidence. More concretely, a w of 0.2 implies that for two sets to be easily discriminable they need to differ by about 40%, as for example in 10 versus 14. With this single free parameter, the model of the internal number line, being it either logarithmic with fixed noise or linear with increasing noise, achieves a remarkable level of fit of empirical data (see Dehaene 2007 for a review).

This value is around 0.15 in both occidental adults and people in remote cultures tested with a larger-smaller and same-different numerosity judgment task (Piazza and others 2004; Pica and others 2004). Pica and collaborators tested a group of indigene people from the Amazon, the Mundurucus, who speak a language with a numeric lexicon restricted to numerals 1 to 5 on a comparison task with large numerosities exceeding the limit of their lexicon (Pica and others 2004). In Mundurucu, w was equal to 0.17, comparable to occidental adults performing the exact same task.

The precision of the internal representation of number increases over lifetime, with a dramatic refinement over the first year of life, extending gradually until late childhood, following a classical developmental trend well described by a power function (Halberda and Feigenson 2008; Piazza and others 2008) (see Fig. 4).

Hence, infants can detect changes in numerosity for ratios of 2:1 at six months (e.g., 4 dots vs. 8 dots)

(Xu and Spelke 2000; Lipton and Spelke 2003) and 3:2 at 9 months (8 vs. 12) (Xu and Arriaga 2007). Recently we tested kindergartners, 10-year-olds, and young adults on a numerosity comparison task. Performance showed that w decreased exponentially from about 0.40 at age 5 to 0.25 at age 10 and 0.15 in adults. These results are quantitatively similar to (Halberda and Feigenson 2008; Piazza and others 2008). The cause of the reduction of w with age is, however, still not known. It could reflect purely maturational processes, but also a contribution from the teaching of counting and arithmetic, which typically starts in kindergarten. However, the observation of a similar w across cultures and in particular in cultures where children do not undergo formal teaching of counting and arithmetic makes the latter hypothesis less likely.

In sum, very simple psychophysical tasks can be used to assess the refinement of the internal representation of numerosity, which, in turn can be readily explained by the functioning of the number-selective neurons of the intraparietal sulcus. In contrast, however, not much is known about the neural processes leading up to the number-selective code in the hIPS, that is, the neuronal mechanisms that allow to convert sensory stimulus into a number-selective coding system.

Multiple Codes for Numbers in the Parietal Cortex

Computational models of numerosity representations have hypothesized at least two intermediate steps between the sensory stimulus and the emergence of the numerosity-selective representation (Dehaene and Changeux 1993; Grossberg and Repin 2003; Verguts and Fias 2005). First, objects are normalized for their appearance (size, shape, color) and summed up to produce an approximate representation of the total number by "accumulator units." The output of these units is then thresholded by increasingly less sensitive units so that the emerging code is number selective. The intuition that some sort of accumulator mechanism is a fundamental step for abstracting numerosity is present in most models of numerosity representation (Gallistel and Gelman 2000). Although the initially discovered number neurons were selective to number, it is only recently that electrophysiological recordings in macaque monkey LIP confirmed the existence of number neurons with an accumulator-like coding scheme (Roitman and others 2007). This elegant study was set up so that it was possible to dissociate sensitivity to number from sensitivity to space, salience, reward expectation, and motor preparation (all dimensions that are potentially coded by LIP neurons). The LIP neurons coding for number differ substantially from the number neurons previously individuated in

the macaque VIP and in the cat posterior neocortex (Thompson and others 1970; Sawamura and others 2002; Nieder and Miller 2004). First and most important LIP neurons are numerosity *sensitive, and not selective*: Rather than showing a specific preference for a given number, they all code monotonically with the number of objects present in their visual field, some by increasing and others by decreasing in firing rate with the logarithm of the number. A second, important difference with numerosity-selective neurons is that the numerosity-accumulator neurons have limited retinotopic receptive fields and only code for the items presented in their receptive field, not for the total number of element present in the display. LIP lies more dorsally and caudally with respect to VIP, and its functional properties differ importantly from VIP neurons: They typically code for space in eye-centered coordinates and code monotonically information integrating over time, space, and reward (Roitman and Shadlen 2002; Hubbard and others 2008) for a review.

The LIP numerosity accumulator code is thus likely to act like an intermediate code in the extraction of the information from the sensory stimulus, and likely to project the information to the VIP neurons upstream in the hierarchical processing of (visual) information (see Fig. 5). As reviewed above, the neural code for number in VIP is quite abstract and likely to respond to auditory as well as to visual numerosity. It is not known if LIP number neurons only respond for stimuli in the visual modality or not. Given that within sensory regions there are accumulator-coding neurons for nonnumerical quantities (Bendor and Wang 2007), it is possible that each sensory system contains some accumulator neurons that are also sensitive to number.

Although the possible human analogous to the monkey numerosity-accumulator neural code has yet to be identified, recent behavioral studies bring indirect evidence for the existence of a similar mechanism in humans (Burr and Ross 2008). In the later experiment, participants were adapted with arrays of different numerosities presented either in their left or right visual field. After viewing these arrays for 30 seconds, participants showed a strong aftereffect distorting their perception of the numerosity of subsequently presented sets: Those containing fewer dots than the adaptation stimulus were illusory, perceived as even less numerous, whereas those with more dots were perceived to be even more numerous. This effect extended to numerosities extremely distant from each other (i.e., 30 and 200) and thus cannot be explained by a numerosity-selective representation. Furthermore, it is restricted to the location of the visual field where the adapter has been presented, in accordance with the property of LIP neurons showing limited response fields.

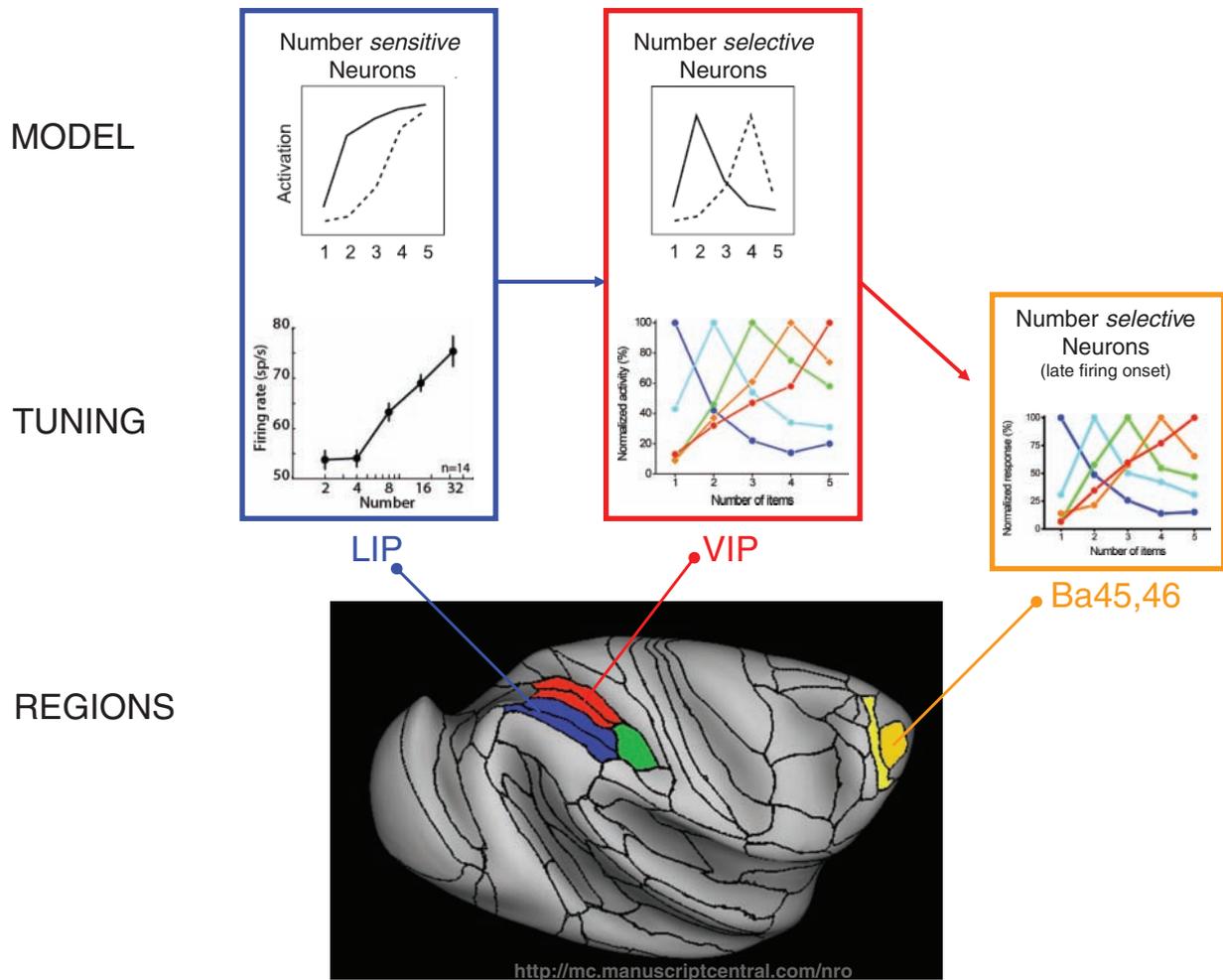


Figure 5. Pathways for numerosity processing in the macaque brain: anatomical and functional characterization. Blue panel: top, theoretical tuning curves of the accumulator stage predicted by computational models (Dehaene and Changeux 1993; Verguts and Fias 2005); bottom, tuning curves of accumulator neuron recorded in the lateral intraparietal (LIP) (Roitman and others 2007). Red panel: top, theoretical tuning curves of the numerosity-selective stage predicted by computational models (Dehaene and Changeux 1993; Verguts and Fias 2005); bottom, tuning curves of numerosity-selective neuron recorded in the ventral intraparietal (VIP) (Nieder and Miller 2004). Orange panel: tuning curves of numerosity-selective neuron recorded in the prefrontal cortex, Brodmann's areas 45 and 46 (Nieder and others 2002 #3622). Bottom figure: monkey LIP, VIP, and Brodmann's areas 45 and 46.

Are the Parietal Codes for Numbers Specific?

A final intriguing question is if the parietal regions for numbers are specialized for numbers or simply code for quantity and/or ordered continua (Cohen Kadosh and others 2008). Several fMRI studies contrasted intraparietal activations during numerical judgments versus other judgments of continuous dimensions such as size, luminance, angle, and other ordered sequences such as letters (Fias and others 2003; Pinel and others 2004). Results show considerable overlapping activation among number and physical size (Pinel and others 2004), and among numbers and letters (Fias and others 2003). Interpretation in terms of neuronal coding must remain extremely cautious. With fMRI, and especially using such simple subtraction designs as is the case for the papers reported

above, we are very far from accessing the micromaps level of coding that might reveal domain specificity. Moreover, even in principle it is not clear which level of precision is needed to test claims for specificity (voxels, columns, or single neurons). Electrophysiological recording in monkeys simultaneously engaged in numerosity and line length discrimination tasks shows that VIP neurons coded for both dimensions (Tudusciuc and Nieder 2007). Even if most neurons coded selectively for either one or the other quantity, about 20% coded for both. Interestingly, their magnitude code was not consistent across domains (neurons tuned for small numbers were not necessarily also tuned to short lines). These results confirm the suggestion from Pinel and colleagues that there is a partial overlap between neural population engaged in processing different quantitative dimensions (Pinel and others 2004).

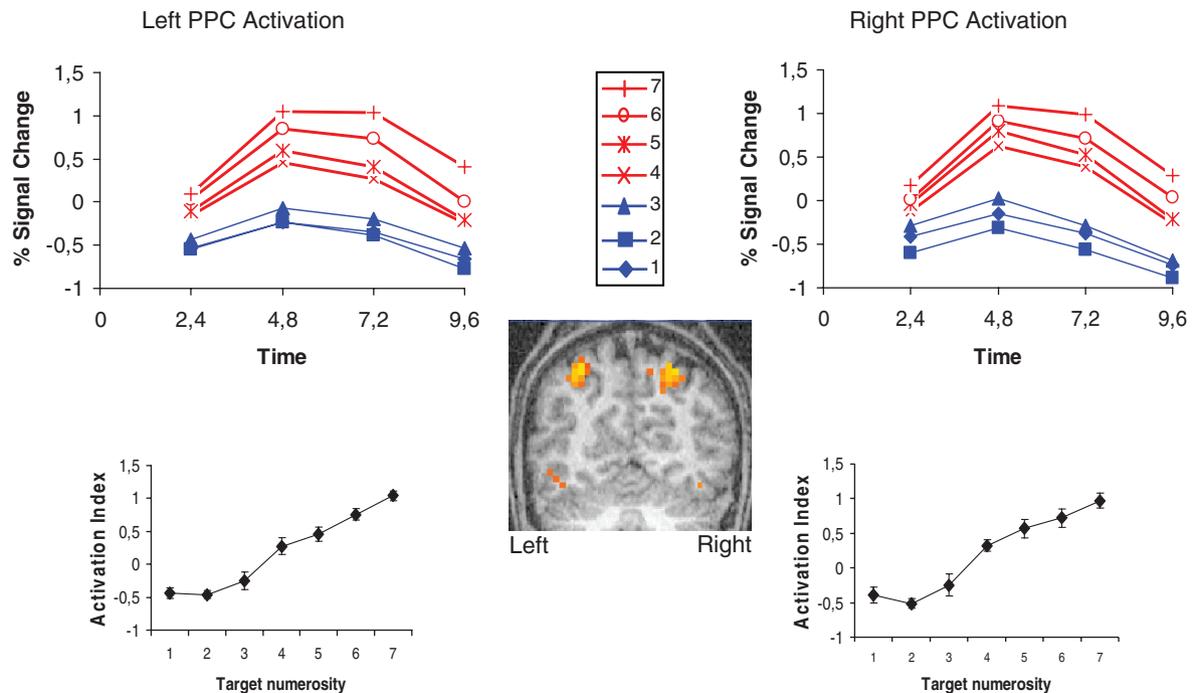


Figure 6. Different involvement of the posterior parietal cortex in counting and subitizing processes. Graphs on the top show the time course of activation in the left and right posterior parietal cortex. Bottom: mean activation level for each stimulus type. Error bars indicate SEM.

Exact Representation of Small Numerosity

There is evidence that small numbers (collections of 1, 2, or 3 objects) receive a special treatment. In infants, for example, adaptation paradigms have revealed an opposite pattern of results depending on whether tested with small or large numerosities: When presented with large sets, they are clearly sensitive to numbers and not to nonnumerical continuous parameters (e.g., total amount of stuff; Xu and Spelke 2000; Brannon and others 2004). In contrast, with small sets, the pattern is reversed: They strongly react to changes in continuous parameters, such as when those are carefully controlled for, they fail to react to number (Feigenson and others 2002). In a quite different task, where the experimenter puts objects, one at a time, inside a box and ask infants to search in the box to retrieve the items, 14-month-olds clearly succeed, even in the presence of major changes in the continuous variables. However, this success shows a clear limit with respect to the size of the numbers: Infants successfully discriminate 1 from 3, but fail to discriminate 1 from 4 (Feigenson and Carey 2005).

In sum, when infants are presented with small sets, their pattern of responses diverges from the characteristic ratio-dependent discrimination observed with large numbers: They are very precise but only up to a certain (small) number. These data are well explained by assuming that small arrays primarily activate a system for representing and tracking distinct individuals that

allows for computations of either their continuous quantitative properties or the number of individuals (Feigenson and others 2004). Theoretically, this dissociation can be accounted for by two alternatives: Either the approximate system does not respond at all in presence of small sets or it does but the resulting representation is not accessed because it is masked by more salient representations. We used a neuroimaging method to address this question, because this method enabled us to access implicit representations directly (Izard and others 2008a). The results showed a clear continuity in the brain response for both large (4–12) and small (2–3) numerosity ranges, supporting the hypothesis that small numbers do enter in the approximate number representational system.

In nonhuman animals, similar set-size limitations have been sometimes observed (Hauser and others 2000), but contradictory evidence has also been reported, maybe indicating that, as infants, nonhuman animals possess the representational resources to overcome these set-size limitations. Monkey neural data also support this idea, showing that the precision of the tuning curves for numerosity extends smoothly over the whole range of all numerosities tested, from 1 to 30 (Nieder and Merten 2007).

In human adults, there is only one very specific case in which small numbers are responded to in a special way: It's when the items are presented *simultaneously*, in *different spatial locations*, and *pop-out* from the background, thus not requiring serial scanning of the display (Trick

and Pylyshyn 1993). In this case, enumeration is fast and accurate for sets of up to three or four items (a phenomenon called “subitizing”) but shows a sudden and linear increase in the number of errors and in reaction times beyond this range (Trick and Pylyshyn 1993; Revkin and others 2008). Neuroimaging data have complemented the evidence for this dissociation by showing that the activation of the posterior parietal cortex, reflecting spatial attentional shifts, shows a sudden and linear increase from numerosity 4 only, and accurately predicts the subitizing capacity across subjects (Piazza and others 2003) (see Fig. 6).

In contrast, when items are presented sequentially, or in layouts that inhibit pop-out, the evidence for different processes for small versus large numbers disappears, and clear signatures of the approximate system are evident: The coefficient of variation (the ratio between the standard deviation and the mean of response distribution) is constant across all numerosities, within and beyond the proposed subitizing range (1–3 to 4; Cordes and others 2001).

While not denying the existence of the subitizing phenomenon, our current hypothesis is that it does not reflect a particular module dedicated to small numerosities but rather a characteristic of the visuospatial system, possibly localized in the posterior parietal cortex, that automatically generates map(s) of a limited number of salient locations in the visual field (Gottlieb 2007). Thus, enumeration of small sets can be readily performed by reading out the total number of peaks of this map. Other tasks involving individuation of multiple items, like, for example, visuospatial memory tasks (Todd and Marois 2004), could rely on such maps. Indeed, PPC activation reflects both subitizing and visuospatial short-term memory capacity (Piazza and others 2003; Todd and Marois 2004).

More generally, although this system for tracking a limited number of objects enables infants, animals, and perhaps adults to solve some numerical tasks in an exact fashion in the small-number range, it does not give an explicit representation of numerosity, contrary to the approximate system. It is only numerical inasmuch as the objects tracked can enter numerically relevant computations.

Exact Representation of Large Numerosity

If the number exceeds the limit of subitizing (see above), to get an exact estimate, subjects have to process each item individually (or in small, subitizable groups) and put them in one-to-one correspondence with more abstract representations. There are at least two crucial mechanisms involved in this complex operation. The first one is the individuation of items. As seen before, our visual system does not allow individuation

of more than a certain small number of items in parallel in a single glance. Thus, when the items exceed this limit (i.e., where there are more than 3 or 4), ocular movements are necessary. Indeed, counting, but not subitizing or estimation, is essentially made impossible if ocular and/or attentional movements are prevented (Oyama and others 1981). The crucial role of serial scanning in counting is confirmed in patients with simultanagnosia, a disorder usually occurring after bilateral parietal damage causing impairments of the serial analysis of a visual scene, with spared perception of individual objects. Those patients are also severely impaired at counting the exact number of objects in visual arrays but not at subitizing or at estimating their approximate number (Demeyere and Humphreys 2007). Imaging and TMS studies have also highlighted the role of the dorsal stream (posterior parietal and lateral premotor cortices) in the serial deployment of attention over different locations of space and/or time, and also possibly reflecting automatic activation of finger counting as a vestige of developmental associations (Butterworth 2000; Piazza and others 2003; Piazza and others 2006).

The second crucial component of counting is working memory, needed to keep the running total while integrating the successive items. In hearing subjects, this is mainly performed by the verbal system, and specifically by the subvocalization component (Logie and Baddeley 1987). Indeed, several imaging studies of counting showed activation in Broca’s area, in the primary motor cortex in the mouth region, and right cerebellum, all associated with internal speech (Hinton and others 2004). Deaf children perform identically to hearing children on this task, using their visuospatial rehearsal loop (Leybaert and Van Cutsem 2002). Contrary to estimation and small numerosity apprehension, the counting mechanisms have no equivalent in nonhuman animals, are not universal among human cultures (Gordon 2004; Pica and others 2004), and are acquired very progressively in an effortful process by human children (Wynn 1990). Typically, children begin to learn the counting routine around the age of two, and in a couple of months, they recite the first numbers in order while pointing to objects. However, they do not seem to understand the meaning of this routine, as, for example, when asked to give the experimenter a certain number of objects (the give-A-Number task; Wynn 1990), they just grab a handful. Progressively, they differentiate “one” from all other numbers, then they learn “two,” and then “three.” This process extends over 1 1/2 years, until the child discovers the meaning of counting and of numbers, and therefore becomes suddenly able to give any number of objects. As a comparison, Matsuzawa trained a chimpanzee to associate Arabic digits to quantities of dots (Matsuzawa 1985). The animal eventually learned all the symbols up to 9 but, contrary to human children, never experienced

any kind of insight that enabled her to accelerate the learning of the next symbols.

Counting therefore appears as a uniquely human activity, and a cultural invention. However, animals, or preverbal infants, or people living in cultures lacking symbols for large numbers could still understand some aspects of the concept of exact number (Izard, Pica, and others 2008). Even though they do not have a procedure for counting in their culture, speakers of the Amazonian or Australian language make use of one-to-one correspondence strategies to reproduce numerosities (Frank and others 2008) and in more complex tasks where the cardinal needed to be tracked through some transformations that changed the identity of the individual objects forming the sets. These tasks tap a knowledge of exact equality, which seems to be universal among humans and can provide a precursor to the development of exact numbers.

Conclusions

Humans come to life equipped with an evolutionary ancient system, based on a bilateral parietal neural circuitry for representing numerosity in an approximate and compressed fashion. During early childhood, through counting and subitizing, symbols for numbers are progressively mapped onto the core representation of numerical quantity, so that by the age of five, children entertain some solid intuitions about the meaning of symbolic number and operations, based on their approximate system (Gilmore and others 2007). Indeed, the success at mathematics later in school highly correlates with the precision of the approximate system for numerosity (Halberda and others 2008). However, the acquisition of the numeric symbols does not simply consist in a direct mapping between the core parietal system for numerosity and symbols for numbers but entails profound changes to the cerebral network processing numerosity (Piazza and others 2007). These changes mostly consist in a progressive refinement of the representation of numerical symbols, in particular, in the left hemisphere. First, during development, there is a progressive shift from a predominance of the right hIPS to a bilateral involvement in both nonsymbolic and symbolic number processing (Ansari and others 2006; Cantlon and others 2006; Piazza and others 2007; Izard and others 2008a). This may well result from the development of linguistic representations for numbers within the left hemisphere. Indeed, in adults, indirect measures of tuning curves for numerosity suggest a more precise representation in the left compared to the right hIPS. Finally, Arabic digits are coded with a higher degree of precision than numerosity, in the left hemisphere more than in the right hIPS (Piazza and others 2007). These observations suggest that during

development language may act as a categorical “boundary sharpener,” thus increasing the precision of the representation of numerical quantity, but only in the linguistic hemisphere.

Some children experience a specific deficit in learning mathematics, while showing IQs within a normal range, a deficit known as dyscalculia. This deficit has been linked to a malfunction of the approximate number system, an idea confirmed by the observation that dyscalculia of different origins results in structural and/or functional impairments at the level of the hIPS (Price and others 2007). Our knowledge of the functional characteristics of the numerical representations localized in the hIPS should guide research to gain a better understanding of this deficit, as well as normal development.

Acknowledgments

VI is supported by an NSF grant to Elizabeth Spelke. The authors thank Stanislas Dehaene, Lola de Hevia, Philippe Pinel, Ed Hubbard, and David Melcher for useful discussions.

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