

Effects of development and enculturation on number representation in the brain

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Abstract | A striking way in which humans differ from non-human primates is in their ability to represent numerical quantity using abstract symbols and to use these 'mental tools' to perform skills such as exact calculations. How do functional brain circuits for the symbolic representation of numerical magnitude emerge? Do neural representations of numerical magnitude change as a function of development and the learning of mental arithmetic? Current theories suggest that cultural number symbols acquire their meaning by being mapped onto non-symbolic representations of numerical magnitude. This Review provides an evaluation of this contention and proposes hypotheses to guide investigations into the neural mechanisms that constrain the acquisition of cultural representations of numerical magnitude.

Numerical magnitude

The total number of items in a set. It can be either exact or approximate, depending on whether the sets are counted or the total number of items is estimated.

Numerical distance

The difference between two numbers. For example, the numerical distance between eight and five is three. Many studies show that numerical distance has a profound effect on the time it takes to make a relative-numerical-magnitude judgement.

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Humans share with non-human primates¹⁻⁶, birds^{7,8} and amphibians⁹ the ability to discriminate numerical magnitudes. The parameters that underlie number-discrimination abilities have been clearly delineated and are similar across species and across development^{10,11} (FIG. 1). The so-called 'number sense' (REFS 11,12) therefore probably has a long evolutionary history. The ability to discriminate numerical quantity might have served functions that are important to survival, such as making foraging decisions or discerning the number of approaching predators¹³.

However, the basic ability to discriminate numerical quantities cannot fully explain the entire extent of human numerical and mathematical skills. In human history, a large set of uniquely human competencies emerged that provided us with the ability to process abstract numerical symbols (such as number words and Arabic numerals) and perform mental arithmetic using these new 'mental tools'.

Most of the current research into the neuroscience of numbers is focused on the neural correlates of the basic representation of numerical quantity in the brain; there is also growing exploration of the relationship between numerical processing of quantity and visuo-spatial processing¹⁴⁻¹⁶. Thus far, investigations into the basic neural representation and processing of numerical magnitude and into the acquisition of symbolic representations and calculating ability have been conducted in relative isolation from one another, and it has often been assumed that symbolic representations are mapped onto pre-existing non-symbolic representations of number.

This Review provides a synthesis of these different strands of research and reassesses the hypothesis that symbolic number representations acquire their numerical meaning through being mapped onto non-symbolic representations. In addition, the Review integrates data from computational modelling, functional neuroimaging and single-cell recording studies to formulate hypotheses for future studies that aim to increase our understanding of the complex interactions that occur between culture and biology in the construction of the brain processes that underlie mathematical skills.

The IPS and numerical-magnitude processing

Data from brain-damaged patients, single-cell recordings and functional neuroimaging have implicated the intraparietal sulcus (IPS) as the crucial area for the processing of numerical magnitude. In order to understand how such parietally mediated processes might shape the acquisition of numerical symbols and mental arithmetic skills, I first discuss the current understanding of the functioning of this brain region during basic number processing.

Neural correlates of quantity representation. When adults determine which of two Arabic numerals is numerically larger, their reaction times and error rates are inversely related to the numerical distance between the numbers^{17,18}. Moreover, when the distance is held constant but the absolute size of the two numerical quantities is increased, reaction time increases and

accuracy decreases^{19–21}. These distance and size effects have become litmus tests for determining the nature of basic representations of numerical quantity²².

Functional MRI (fMRI) studies^{19–21} have revealed that activation in bilateral regions of the inferior parietal

lobules — specifically, the IPS (FIG. 2) — negatively correlates with numerical distance. This finding has been frequently replicated^{23–26}, and recent data suggest that the relationship between numerical distance and IPS activity is disrupted in children with developmental dyscalculia²³ (BOX 1).

Numerical distance also negatively correlates with activation in bilateral prefrontal and precentral regions, suggesting the involvement of fronto-parietal networks in the processing of numerical magnitude^{27,28}. Although some studies²⁹ have attempted to delineate the similarities and differences between prefrontal and parietal activation during numerical-magnitude processing, the focus has primarily been on the IPS³⁰. Methodological advances such as Dynamic Causal Modelling³¹ and Grainger Causality Modelling³² of fMRI data should facilitate research on network-based representations of numerical magnitude.

Single-cell recordings from neurons in the prefrontal and parietal cortices^{33,34} in monkeys (FIG. 2c) have also provided significant insight into the neural correlates of numerical-magnitude representation. In a delayed match-to-sample task (FIG. 2d), monkeys were trained to judge whether a sample numerosity (an array of dots) differed from a target numerosity. Populations of neurons in the prefrontal cortex (PFC) and IPS preferentially fired during the presentation of a particular numerosity. Hence, these cells seem to represent cardinal values or specific places on the ‘mental number line’ (also known as place coding or ‘labelled line’ coding). Interestingly, the firing rate of these neurons decreased monotonically as the numerical distance between the preferred and the presented numerical magnitude increased (FIG. 2e). The firing properties of these ‘number neurons’ in the monkey PFC and IPS explain the distance effect, as the tuning curves of neurons with preferred numerosities that are separated by a small numerical distance overlap more than those of neurons with preferred numerosities that lie far apart. Consistent with the size effect, neurons with a high preferred numerical magnitude have wider tuning curves than neurons with a low preferred numerical magnitude^{33,34} (FIG. 2f).

Number neurons in the prefrontal and parietal cortices have similar basic response properties, but their temporal response properties differ³⁴: IPS neurons respond earlier than PFC neurons, suggesting that numerical quantity might be extracted in the IPS and sent forward to the PFC for the implementation of number-related responses.

Modules in the brain or distributed patchworks? There has been much debate over the extent to which the IPS contains a number module³⁵. In humans, processing of symbolic (for example, Arabic numerals) and non-symbolic (for example, arrays of dots) representations of numerical magnitude triggers similar neural activation in the IPS, indicating that this brain region might house a number module^{23,36}. However, it is unclear whether the IPS only processes numerical magnitude — in other words, whether there is domain-specific representation of numerical magnitude in the IPS. Indeed, in a series

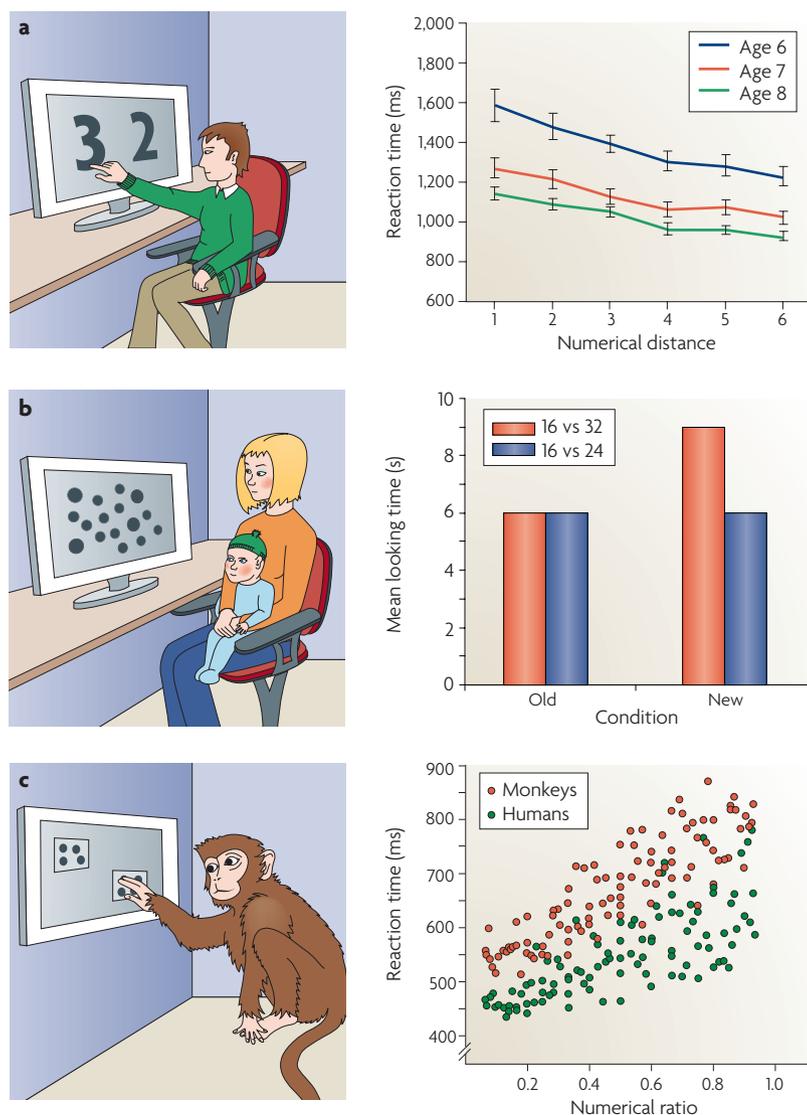
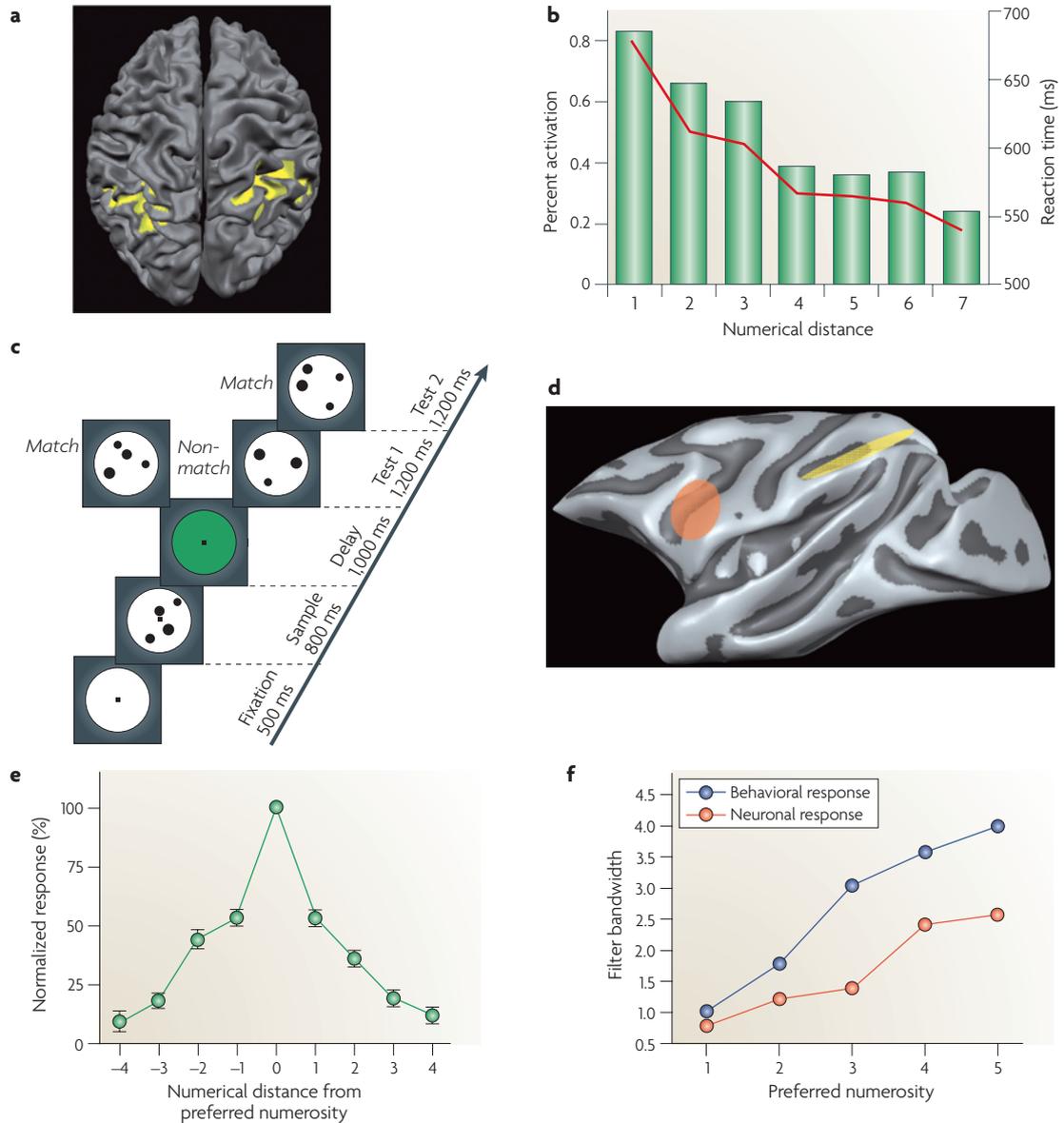


Figure 1 | Ontogenetic and phylogenetic continuity in basic signatures of numerical-magnitude representation. **a** | When children and adults compare which of two numerical stimuli is numerically larger, there is an inverse relationship between numerical distance and reaction time; this is known as the distance effect¹⁷. Furthermore, reaction times are positively correlated with the absolute size of the numerical stimuli (the size effect). The distance effect exists in both children and adults, but it decreases in strength with age^{128,129}. **b** | When six-month-old infants are presented with repeated presentations of large numbers of dots, their looking time decreases (habituation). When looking times to old (habituated) and new numerosities are subsequently compared, the infants' ability to distinguish between old and new numerosities is dependent on the distance between the numerical magnitudes^{130,131}. For example, Xu¹³² found that 6-month-old infants are sensitive to the difference between 16 and 32, but fail to discriminate between 16 and 24. **c** | Rhesus macaque monkeys can learn to order pairs of numerosities by numerical magnitude by touching them sequentially on a touchscreen. The accuracy and speed with which the animals can do this depends on the ratio of the numerosities. The similarity in the performances of monkeys and humans suggests that there is a high degree of phylogenetic continuity in basic representations of numerical magnitude. Part c reproduced, with permission, from REF. 3 © (2006) Blackwell Publishers.

of three fMRI experiments reported in one paper³⁷, IPS activation was similar during non-symbolic numerical-magnitude processing and non-numerical control tasks, suggesting that the IPS might not house a domain-specific representation of numerical magnitude.

The idea of domain-specific brain representation rests on the assumption that a single region (in this case the IPS) is involved in a particular type of stimulus processing and responds to the stimulus category regardless of the presentation format (symbolic,



Numerosity

A term used to describe non-symbolic representations of numerical magnitude (such as arrays of dots or squares).

Cardinal number

The last number in a sequence; cardinal numbers represent the total number of items in a set.

Mental number line

A metaphor for the mental representation of numerical quantity, based on findings that support an association between space and number.

Tuning curve

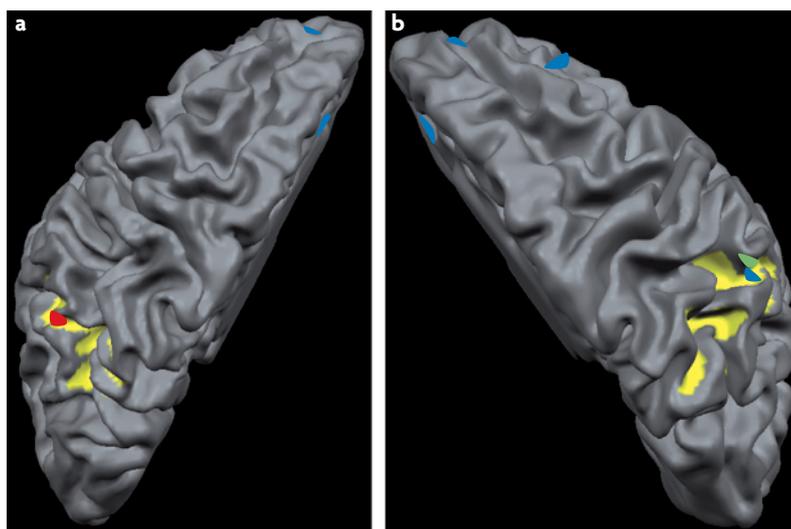
How single neurons or, in the case of fMRI, large populations of cells are tuned to respond to a particular stimulus rather than to other, similar stimuli. A neuron might respond preferentially to three items but also fire during the presentation of one or two items.

Domain specificity

When brain regions respond more to a stimulus from one domain of cognitive processing (for example, faces) than they do to another (for example, houses). Regions that exhibit such domain-specific response properties are thought to be biologically determined to represent and process stimulus categories from a particular cognitive domain.

Figure 2 | Neural correlates of basic numerical-magnitude representation in the human and monkey brain. **a** | Functional neuroimaging studies have implicated the bilateral intraparietal sulcus (IPS; shown in yellow) in numerical-magnitude processing. **b** | Activation in the IPS is negatively correlated with numerical distance during a number-comparison task²⁷. This inverse relationship is similar to the behavioural distance effect (see red line). **c** | Using a delayed match-to-sample task in which the animal has to indicate whether a sample numerosity matches a test display, the 'number sensitivity' of single neurons in the macaque prefrontal³³ and parietal cortices³⁴ (**d**; shown in orange and yellow, respectively) was tested. The data revealed the existence of 'number neurons', which fire preferentially to the presentation of a particular number of dots. **e** | Although number neurons prefer a particular numerical magnitude, their response to other numerosities is related to the numerical distance between the presented and the preferred numerical magnitude, revealing a distance effect at the level of single neurons. Thus, a neuron that was found to prefer a numerical magnitude of three fired slightly less during the presentation of four dots and less still during the presentation of five dots or one dot. **f** | Consistent with the size effect, the degree to which number neurons respond to other numerosities (their filter bandwidth) increases as a function of the size of their preferred numerical magnitude. A similar bandwidth function could be observed for the behavioural data, where monkeys' incorrect classification of non-matching target numerosities increased as a function of the sample numerosity. Part **b** reproduced, with permission, from REF. 27 © (2001) Academic Press. Part **c** reproduced, with permission, from REF. 55 © (2005) Macmillan Publishers Ltd. Parts **d** and **e** reproduced, with permission, from REF. 33 © (2002) American Association for the Advancement of Science.

Box 1 | Neural basis of developmental dyscalculia



It is a little-known fact^{119,120} that approximately 5% (although estimates vary between 3 and 11%) of children who exhibit normal intelligence present a specific and persistent difficulty with calculation and mental arithmetic, called developmental dyscalculia. Compared with developmental dyslexia, there has been little research into the behavioural and neural basis of developmental dyscalculia¹²¹, but behavioural studies suggest that it is associated with impairments of basic numerical-magnitude processing¹²². The few studies that have investigated the neural basis of developmental dyscalculia consistently suggest that there is a pattern of structural and functional alterations in the intraparietal sulcus (IPS) and the prefrontal cortex (PFC) (see figure: yellow indicates the IPS; red, blue and green indicate where structural and anatomical abnormalities have been found in the left (a) and right (b) hemispheres). Isaacs *et al.*¹²³ used structural MRI to compare the brains of children who had low birth weight and who exhibited calculation difficulties with those of children of similar low birth weight but with normal scores on a calculation test. Children with specific calculation difficulties were found to have less grey matter in the left IPS (red area in the figure). A recent comparison of the structural neuroanatomy of children with and without developmental dyscalculia¹²⁴ revealed that children with developmental dyscalculia have less right-parietal grey matter and have grey matter abnormalities in regions of the frontal cortex (blue areas in the figure). A functional neuroimaging study of developmental dyscalculia¹²⁵ did not find any abnormalities in brain activation during number-comparison or calculation in children with dyscalculia, but the children did show lower overall activation during approximate calculation in regions of the PFC and IPS. Another functional MRI study¹²⁶ compared children with dyscalculia with a group of age-matched typically developing peers, using a non-symbolic numerical-magnitude comparison task. Although the non-symbolic numerical distance task significantly modulated activity in the right IPS in the typically developing participants, this effect was absent in the children with developmental dyscalculia (green area in the figure). Consistent with the notion of a right-parietal dysfunction, Cohen-Kadosh *et al.*¹²⁷ found that virtually lesioning the right parietal cortex in healthy adults by means of transcranial magnetic stimulation impaired automatic number processing.

Modularity

A term from cognitive science that refers to the notion that different cognitive domains (for example, language, visuo-spatial cognition and social cognition domains) have distinct organizational principles and are represented in encapsulated modules.

non-symbolic, auditory or visual). As pointed out by Nieder³⁷, this hypothesis is derived from psychological theories of modularity³⁸, and it is not clear how well such assumptions transfer to brain-based modularity of cognitive processing. Furthermore, to establish that a brain region is specifically involved in a particular cognitive process, one needs to compare the engagement of that region during the cognitive process of interest with its activation in response to an infinite number of other stimulus categories and processes — an impossible experimental undertaking.

Two recent fMRI^{39,40} studies offer a different view on the relative degree of specialization of the IPS for numerical magnitude. Both revealed substantial overlap in IPS activity for numerical and non-numerical comparisons of quantity, but both also identified cortical IPS regions that showed relatively stronger activation for numerical than for non-numerical magnitudes. This suggests that the IPS contains a patchwork of areas that have overlapping biases for a particular stimulus category, rather than neatly segregated modules. In the future, multi-voxel pattern analysis^{41–43} might help to elucidate the overlap between representations of non-numerical and numerical quantity in the IPS, the distribution of local biases for particular types of comparison and the reliability of these biases across subjects.

The notion that numerical and non-numerical quantities are represented in overlapping areas of the IPS has been confirmed in single-cell recording studies⁴⁴. Monkeys were trained to discriminate either different numerosities or different line lengths (FIG. 3a); IPS neurons responded to length, numerical magnitude or both, indicating that there is both discrete (numerical) and continuous (non-numerical) coding of magnitude in the IPS, even at the single-cell level. Furthermore, these results suggest that there is no clear topographical segregation between populations of neurons that respond to either discrete or continuous magnitude (FIG. 3b). Another study⁴⁵ found similar common and segregated coding of sequential and simultaneously presented numerical magnitude in the monkey IPS.

Although most current evidence suggests that there are both distributed and overlapping representations of numerical and non-numerical magnitude, one fMRI study⁴⁶ had different results: participants were presented with either different numbers of blue and green squares (discrete, numerical quantities) or with the same display transformed into smoothly changing distributions of green and blue hues (continuous, non-numerical quantities), and were asked to judge whether they saw more blue or more green. There was greater bilateral activation of the IPS during discrete than during continuous quantity judgements, suggesting that at least some parts of the IPS are specific for the representation of discrete quantity.

Importantly, the resolution of fMRI is still severely limited in comparison with that of single-unit recordings and, as discussed above⁴⁴, such recordings have already revealed highly distributed representations of numerical and non-numerical magnitude, as well as format-specific and format-general representation⁴⁵ in the IPS. Thus, it is possible that the fMRI findings that suggest that parts of the IPS are specialized for numerical magnitude might simply reflect the existence of areas in which relatively more neurons code for numerical than non-numerical magnitude. Therefore, even data that show greater engagement for numerical versus non-numerical magnitude processing might be consistent with the notion of distributed networks of activation with local biases. Similarly, a region that responds to both symbolic and non-symbolic representations of numerical magnitude might nevertheless contain neurons that code specifically for one format. In other words, it is currently difficult

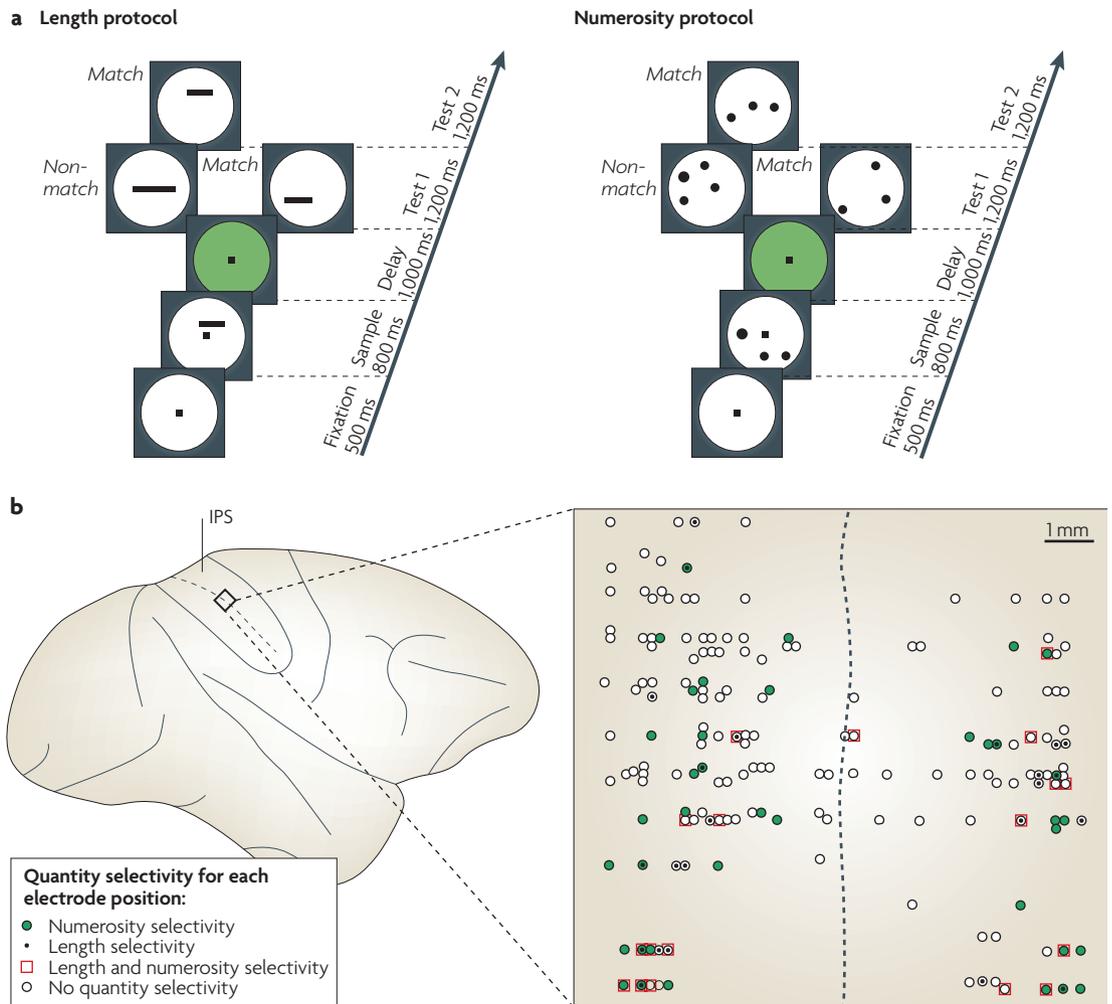


Figure 3 | Distributed and overlapping representations of numerical and non-numerical quantity in the intraparietal sulcus. **a** | Macaque monkeys were trained on a delayed match-to-sample task in which they judged either whether a sample line presented after a delay matched the length of a previously presented line (left panel) or whether the number of dots in a sample array presented after a delay matched the number of dots in a previously presented array (right panel). Responses of single cells were recorded from the intraparietal sulcus (IPS). The data suggest that there are cells that are selective for either numerical magnitude or length, but they also reveal that there are neurons that respond to both. **b** | Interestingly, no topographic organization of numerical-magnitude- or length-sensitive cells could be detected, demonstrating that even at the level of individual neurons in the parietal cortex there is no neat spatial segregation between the representation of numerical and non-numerical quantity. Figure reproduced, with permission, from REF. 44 © (2007) National Academy of Sciences.

to unequivocally localize modules in the brain for particular domains of cognitive processing or for particular stimulus types using fMRI. In addition, given that the parietal cortex is a higher-level association area of the brain with heterogeneous functions^{47–49} that include, among others, grasping⁵⁰, visual attention⁵¹ and working memory^{52,53}, it might be futile to search for spatially localized and dissociable domain-specific representation. It might instead be more productive to investigate how the representation and processing of numerical magnitude in the parietal cortex interacts with other parietally mediated cognitive functions^{14,54}.

Magnitude or order? One should also consider how brain activation during numerical-magnitude processing differs from the representation of other information

that can be embodied by numerical stimuli, such as sequential order⁵⁵. Indeed, tasks that require magnitude processing also involve processing of order-related information⁵⁶. Two recent papers^{57,58} directly compared the neural bases of order and magnitude processing by contrasting brain activation during numerical-magnitude comparisons with brain activation during comparisons of non-numerical stimuli that carry order information (letters and months). They found that the anterior IPS responds equally to both numerical and non-numerical order, suggesting a role for this anterior region of the IPS in the abstract representation of ordinal information that is not number-specific.

Although these data suggest that there is a link between cardinal and ordinal representations of numerical magnitude, data from brain-damaged

Multi-voxel pattern analysis
fMRI data are typically analysed using voxel-wise statistics; multi-voxel pattern analysis uses pattern-classification algorithms to decode fMRI activity that is distributed across multiple voxels.

Ordinality
The rank-order relationships between numbers (for example, the third in line).

patients have revealed double dissociations between the two^{59,60}. Furthermore, a recent event-related potential (ERP) study suggested that order and magnitude processing might have different time-courses in the left and right IPS and in prefrontal regions⁶¹. As was recently suggested⁶², single-cell neurophysiology studies might help us to better understand the extent to which both overlapping and segregated representations of cardinality and ordinality exist at the single-cell level. Nevertheless, the data suggest that the IPS might be involved in domain-general representations of order that are recruited during numerical-magnitude processing.

Symbolic representations of numerical magnitude

Verguts and Fias⁶³ have put forward a model (FIG. 4a) which proposes that symbolic and non-symbolic inputs are transformed into internal place-coded (cardinal) representations by different pathways. Consistent with an earlier computational model⁶⁴, their model predicts that non-symbolic numerosities are transformed by an intermediate step (referred to as ‘summation coding’) into a summed representation that can be represented internally as a place code. Consistent with the accumulator model of magnitude representation⁶⁵, the noise in the summation field is proportional to the number of inputs that are being summed. The Verguts and Fias model

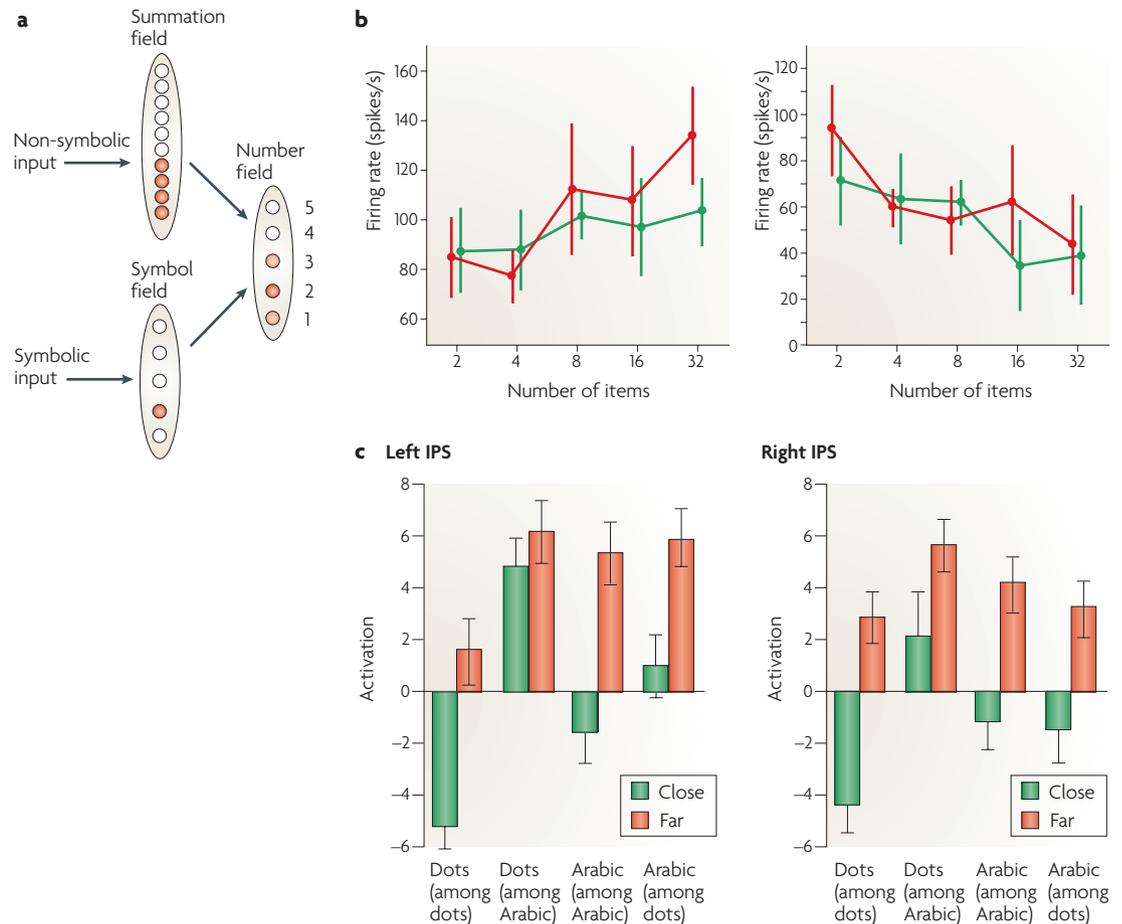


Figure 4 | Different processing pathways for symbolic and non-symbolic numerical magnitude.

a | A computational model⁶³ predicting independent input fields for symbolic and non-symbolic numerical stimuli. Unlike symbolic inputs, non-symbolic stimuli need to be summed before they can be mapped onto the number field. This summation yields size and distance effects because the similarity between input vectors decreases with distance and increases with their relative size. In this model, representations of symbolic numerical magnitude are learned through the simultaneous presentation of symbolic and non-symbolic inputs. Results of simulations suggest that there are sharper representations for symbolic inputs, as the intermediate (hidden layer) summation coding is not required. **b** | Consistent with this model⁶³, neurons in the monkey lateral intraparietal cortex (LIP) exhibit responses that might reflect summation coding: their responses either increase or decrease monotonically as a function of the size of presented non-symbolic numerosities. **c** | Recent fMRI adaptation data⁶⁷ support the notion that symbolic stimuli have sharper representations in the left intraparietal sulcus (IPS) than non-symbolic stimuli. Although both the left and the right IPS responded to symbolic and non-symbolic numerical deviants, the left IPS responded equally to close and far non-symbolic deviants following the adaptation to symbolic deviants. These findings suggest that the coarse representation of both close and far non-symbolic deviants differs from the sharp tuning of the adapted representations of symbolic numerical quantity. Part **a** reproduced, with permission, from REF. 63 © (2004) MIT Press. Part **b** reproduced from REF. 66. Part **c** reproduced, with permission, from REF. 67 © (2007) Elsevier Science.

implicitly predicts how children learn symbolic representation — namely, the representations are acquired after the representational system has learned to associate non-symbolic inputs with internal representations of numerical magnitude. This assumption is based on the finding that even young infants can discriminate between non-symbolic numerical magnitudes, and the model thus proposes that symbolic representations are learned through the simultaneous presentation of symbolic and non-symbolic inputs. This has the consequence that although symbolic inputs do not go through the intermediate summation coding, their representations in the number field are influenced by the simultaneous non-symbolic inputs in such a way that, for example, the presentation of a symbol for the place code '3' leads to slight co-activation of the place codes '2' and '4'. In other words, because symbolic place-code representations are acquired by mapping them onto the coarse (or approximate) place-code representation of non-symbolic magnitudes, the symbolic representations 'inherit' some of the overlapping nature of the non-symbolic place codes. This, according to Verguts and Fias, explains why the distance effect still occurs when symbolic representations of numerical magnitude are compared. However, because the influence of the noisy summation coding on symbolic representations is indirect, the tuning curves for symbolic place codes on the number field are thought to be sharper and the distance effect thus smaller. Recent studies have provided support for some of the different predictions (summation and place coding) of this model^{66,67}.

Evidence for summation coding in the lateral IPS. Recent evidence suggests that there are cells in the monkey lateral intraparietal cortex (LIP; located on the lateral bank of the IPS) that have firing rates that either increase or decrease monotonically with the number of visual elements presented to the monkey⁶⁶ (FIG. 4b). The response properties of these neurons nicely meet the prediction of the 'accumulator model' (REFS 65,68) and are consistent with the idea of summation coding^{63,64}. Consistent with these models, it is possible that these summation-coding neurons in the LIP serve as inputs to the place-coding neurons in the IPS^{33,34,69}, but how summation and place coding are interrelated in the brain remains an open question.

A significant strength of the above study⁶⁶ is that, unlike most single-cell recording studies, it did not require the monkeys to be trained to discriminate numerosity, and therefore the measured neuronal responses are unlikely to be the result of training.

Association of symbolic and non-symbolic magnitude in the monkey PFC. Although non-human primates do not use numerical symbols, they can be trained to associate symbols with numerical magnitudes^{70,71}. A recent study with macaque monkeys⁷² used a delayed match-to-sample method (FIG. 2c) to train the monkeys to both match identical numerosities (arrays of dots) to each other and match numerical symbols (Arabic numerals) to numerosities. In other words, monkeys learned to

associate Arabic numerals with numerosities. Consistent with previous studies³³, neurons in the PFC preferred particular quantities and exhibited size and distance effects. Importantly, many of these cells preferred a particular quantity in both the numerosity–numerosity and the symbol–numerosity matching paradigms, suggesting that prefrontal regions might have a role in mapping abstract numerical symbols onto their quantitative referents. Consistent with the prediction of the model by Verguts and Fias⁶³ that symbolic representations are more distinct and less noisy, the tuning curves of PFC neurons were narrower when symbols (Arabic numerals) were matched with non-symbolic magnitudes than when non-symbolic magnitudes were matched with each other.

By contrast, although neurons in the IPS showed a preference for either symbolic or non-symbolic representations of a particular magnitude, almost none responded to both symbolic and non-symbolic numerical magnitudes⁷². Indeed, only PFC neurons seemed to be involved in the association of non-symbolic and symbolic representations of numerical magnitude. These results might seem to be at odds with the notion that the IPS is crucial for the representation of numerical magnitude in adult humans⁷³. However, it is possible that the association between non-symbolic and symbolic representations of numerical magnitude in the adult human IPS is the result of learning and developmental processes. Consistent with this hypothesis are recent neuroimaging studies^{28,74} which show that children recruit more prefrontal regions during symbolic number processing than adults. Thus, during human brain development and the acquisition of linguistic competencies, parietal regions might specialize for the representation and processing of the association between numerical magnitudes and abstract symbols. It remains to be seen whether such a shift can also be revealed in non-human primates following more extensive training.

It should be noted that the type of training that was used in this study with monkeys assumes that symbolic representations of numerical magnitude emerge as a function of their pairing with non-symbolic representations, such as arrays of dots (as does the Verguts and Fias model). The extent to which these findings can be generalized to the brain mechanisms that subservise the acquisition of numerical symbols in humans depends entirely on the validity of this assumption.

Representation of symbolic magnitude in the human brain. The above data suggest that, in monkeys, neurons that code for non-symbolic magnitudes have slightly different response properties to those that code for symbolic magnitude. Specifically, the prefrontal and parietal neurons that respond preferentially to a symbolic numerical magnitude have narrower tuning curves than neurons that respond to a non-symbolic magnitude. Similarly, a recent neuroimaging study⁶⁷ provides evidence for more precise coding of symbolic than non-symbolic numerical magnitude in humans; however, in contrast to monkeys, humans had narrower tuning curves for symbolic representations in the left IPS rather than in the PFC.

Accumulator model of numerical-magnitude representation

A model of numerical-magnitude processing in which enumeration involves the passing of impulses through a gate into a summed representation. This summed representation can be likened to a measuring cup: in this analogy the level of the accumulated impulses represents the total number of enumerated impulses. This is also referred to as 'summation coding'.

Participants were presented with trains of either arrays of dots (non-symbolic magnitudes) or Arabic numerals (symbolic magnitudes) of a constant numerical quantity. Infrequently, numerical deviants of either format were presented. The repetition of a given numerical quantity led to a reduced response in the bilateral IPS regardless of the presentation format (FIG. 4c). Consistent with earlier findings⁷⁵, the deviants led to a recovery in IPS activation that was proportional to the numerical distance between the habituation and the deviant numerical magnitude. Interestingly, this distance-dependent recovery occurred both when deviant Arabic numerals were presented among dots and when deviant numbers of dots were presented among Arabic numerals, suggesting that adaptation is notation-invariant.

In addition, there was a hemispheric difference: following adaptation to an Arabic numeral, deviant dot arrays that were far removed (in terms of numerical quantity) from the repeated Arabic numerals and deviant dot arrays that were of similar (close) quantity induced an equal amount of dishabituation in the left IPS but not the right IPS (FIG. 4c). This suggests that there is greater precision of coding (or narrower tuning curves) for symbolic representations of numerical magnitude in the left IPS than in the right IPS.

More evidence suggesting that there might be notation-specific symbolic representation of numerical quantity in the parietal cortex comes from another fMRI adaptation study⁷⁶ in which activation of the left IPS decreased as a function of the number of repeated presentations of the same numerical magnitude regardless of format, whereas repetition-induced suppression of activity in the right parietal cortex was found only for Arabic numerals (not for number words).

In summary, the symbolic representation of numerical magnitude in the human left IPS might be more precise than the representation of non-symbolic numerical magnitude. Moreover, symbolic representations in the parietal cortex might be format-specific. These data therefore suggest that the acquisition of symbolic representations of numerical magnitude either changes pre-existing representations or leads to the construction of novel, format-specific representations of numerical magnitude in the IPS.

How do symbolic representations emerge?

Taken together, the data suggest that the symbolic representation of numerical magnitude involves processes that are different in subtle ways from those that are engaged by non-symbolic numerical stimuli, and that there might be multiple representations for different symbolic formats (such as Arabic numerals and number words). These models and data therefore demand careful re-evaluation of the commonly held assumption^{10,77,78} that representations that are tapped by non-symbolic stimuli are the sole building blocks for higher-level, symbolic representations. Thus far, both computational models^{63,78} and training studies⁷² have assumed that the development of the ability to represent and process numerical symbols involves a process by which symbolic representations of numerical

magnitude are mapped onto pre-existing non-symbolic representations. A plausible alternative possibility, however, is that non-symbolic and symbolic representations of numerical magnitude draw on different neurocognitive processes. It has been argued that approximate representations of numerical magnitude might not serve as adequate representational precursors to exact representations of the integer list⁷⁹.

Some data already suggest that symbolic representations of numerical magnitude might be different from non-symbolic representations. For example, Polk *et al.*⁸⁰ reported that a patient with damage to the left supramarginal gyrus (SMG) was severely impaired on symbolic but not non-symbolic magnitude processing. Moreover, a recent cortical-stimulation study⁸¹ revealed that the SMG is associated with Arabic-number reading, suggesting that this area has a role in processing symbolic representations of numerical magnitude.

Furthermore, a recent investigation⁸² in two-to-four-year-old children suggested that the process of approximate numerical-magnitude representation is independent from a child's developing understanding of the meaning of counting (the 'cardinality principle'). Specifically, LeCorre and Carey⁸² found that some children can count out exactly eight and nine objects when asked to do so but did not use the number words 'eight' or 'nine' when asked to estimate rapidly presented arrays of eight-to-twelve dots, indicating that the children had not yet approximately mapped number words onto large non-symbolic numerosities. In other words, such mapping does not seem to be a necessary and sufficient prerequisite for children's developing understanding of the functional significance of the count sequence. Instead, it has been argued that the ability to rapidly enumerate small numbers of objects ('subitizing') might be a crucial scaffold for the acquisition of an exact, integer-list representation of number^{79,82}.

This study also raises an often neglected point: children acquire the meaning of number words before they learn the visual symbols that represent numerical magnitudes (that is, Arabic numerals); it might therefore be the case that children map visual symbols onto earlier-developed representations of auditory number words, rather than directly onto non-symbolic representations of numerical magnitude.

More evidence for potential qualitative differences between symbolic and non-symbolic representations of numerical magnitude is provided by a recent study which showed that children with developmental dyscalculia are impaired on symbolic but not non-symbolic numerical-magnitude comparison⁸³.

Interestingly, the 'numerosity code' (REFS 84,85) computational model of numerical-magnitude representation does not assume that there is a tight coupling between symbolic and non-symbolic representations of numerical magnitude and might therefore model symbolic representations that are not a direct consequence of mappings onto non-symbolic representations of numerical magnitude. This model posits that each numerical magnitude is represented as a set of activated units (summation coding). However, in contrast to other

fMRI adaptation

A phenomenon whereby repeated presentation of a particular stimulus leads to reductions in the fMRI signal in brain regions that are involved in representing and processing that stimulus. It is also referred to as 'repetition suppression'.

models^{63,64} that have incorporated summation coding, this model posits that summation-coded representations of numerical magnitude are not noisy or approximate, but discrete, linear and exact. Such properties fit well with the symbolic representations that are used to compute the exact results of, for example, mental-arithmetic problems. According to this model, distance and size effects emerge as a consequence of a nonlinear decision process rather than from an approximate representation of numerical magnitude and noisy summation codes. Note that this model does not assume that place coding of numerical magnitude is the representation of exact number, but instead proposes that summation coding is discrete. The numerosity code currently does not offer a developmental perspective and hence it is unclear how this representation develops as a function of experience with numerical symbols.

Neural correlates of mental arithmetic

Once symbols (spoken number words and numerical symbols (for example, Arabic numerals)) have been mapped onto internal representations of numerical quantities, these symbolic systems can be applied to invented algorithms to solve, for example, arithmetic operations.

Work on the brain mechanisms that underlie mental arithmetic has a long history. In 1919 Henschen reported a strong association between damage to the left parietal cortex and calculation deficits⁸⁶. Furthermore, in 1940 Gerstman⁸⁷ described a group of symptoms (which together comprise Gerstmann syndrome), including acalculia, finger agnosia and left–right disorientation, which resulted from damage to the left angular gyrus, which lies adjacent to the IPS. Since then, a large number of papers have confirmed the role of the angular and supramarginal gyri in calculation^{88–91}. Given the involvement of the left temporoparietal cortex in language and reading⁹², it has been proposed that the activation of these gyri during calculation might reflect the involvement of verbal processes in calculation⁹³. Specific learning difficulties in mathematics (developmental dyscalculia) frequently co-occur with impairments of reading (developmental dyslexia); therefore, it is possible that a common impairment of functions that are subserved by the angular gyrus might underlie this co-morbidity. It is plausible that it is symbol-referent mapping that is impaired, such as mapping between arithmetic problems and their solutions (which are stored in memory), grapheme–phoneme mappings or mappings between abstract numerical symbols and the magnitudes that they represent.

An intriguing aspect of Gerstmann syndrome is the co-occurrence of finger agnosia and calculation deficits following damage to the left angular gyrus. A potential link between finger discrimination and mental arithmetic has been investigated in both children and adults^{94,95}. A recent transcranial magnetic stimulation (TMS) study⁹⁶ demonstrated that transient disruption of the angular gyrus results in impairment to the access of finger schemas, as well as impairment in numerical-magnitude processing. This suggests that childrens' use of finger counting strategies in the early stage of

arithmetic development might leave a 'cortical trace' that is reactivated during mental arithmetic even when retrieval strategies are being used.

Understanding the significance of deactivation during calculation. In most fMRI studies of calculation, the activation that is observed in regions in the left temporoparietal cortex, such as the angular and supramarginal gyri, is in fact due to a difference in deactivation relative to baseline^{97,98}. Thus, greater activation of the angular gyrus — for example, during single- versus multi-digit calculation — is mostly reflective of significantly less deactivation during single-digit multiplication⁹⁹. Interestingly, bilateral regions of the temporoparietal cortex are thought to be part of the so-called 'default' or 'resting-state' network^{100,101}, which exhibits decreases in blood flow relative to baseline during various goal-directed, active tasks. Although deactivations are frequently left undiscussed, it has been shown that the degree of deactivation of brain regions can be tightly coupled to individual differences in performance^{102,103}. Future investigations should provide a better understanding of the role of deactivation in the left temporoparietal cortex during calculation and number processing, its relationship to the 'resting-state' network and its functional significance for symbolic number processing and calculation.

Training-related changes. A recent series of studies investigated the changes in functional neuroanatomy that occur as individuals learn arithmetic problems^{58,104–106}. In one study¹⁰⁴, adults were extensively trained on a set of complex multiplication problems. When they subsequently attempted to solve both trained and untrained problems, activation in the left intraparietal and left inferior frontal regions was greater during untrained-problem solving. The reverse contrast revealed greater activation in the left angular gyrus, indicating a training-related shift in activation from left intraparietal regions to the left angular gyrus (FIG. 5b).

Another study¹⁰⁵ investigated whether relative shifts in activation differ as a function of the particular training method. Specifically, 'training by drill' (rote learning the result of a two-operand problem) was compared with 'training by strategy' (applying an instructed algorithm). Greater activation of the angular gyrus was found during the solving of problems learned by drill than during the solving of those trained using the strategy algorithm. Furthermore, another study found that although the angular gyrus was activated more by trained than by untrained multiplication problems, it did not exhibit training effects for subtraction¹⁰⁶. Thus, the type of instruction and the particular arithmetic operation dynamically modulate the relative activation of intraparietal and left temporoparietal regions during mathematical processing.

Individual differences in arithmetic and the left temporoparietal cortex. The strong association between activity in the left angular gyrus and the learning of exact arithmetic raises the question of whether individual

Finger agnosia

Impairment of the ability to distinguish between fingers. It is associated with damage to the left angular gyrus and frequently co-occurs with calculation deficits.

Two-operand problem

An arithmetic problem involving two numbers (for example, 12×45).

Enculturation

The process (encompassing language development, education, learning, *et cetera*) by which an individual becomes a fully functioning member of his or her culture.

differences in the recruitment of this region are related to individual differences in mathematical achievement. A recent study⁹⁷ indicated that this is indeed the case. Specifically, adults who scored low on a standardized test of mathematics but who had otherwise normal intelligence showed less activation of the angular gyrus during both single- and multi-digit multiplication than their mathematically more able peers⁹⁷. Consistent with the group difference, individuals' standardized mathematics scores correlated with calculation-related activation of the angular gyrus. This association remained significant even after the effect of individual differences in accuracy

and response times were controlled for, strengthening the claim that relative levels of modulation of the angular gyrus during calculation have functional significance and do not merely reflect differences in performance.

Effects of culture and education. To what extent do education and culture lead to changes in the connectivity and relative degree of activation of the brain circuits that underlie numerical and mathematical processing? A recent comparison of native English and Chinese speakers¹⁰⁷ showed different activation and functional connectivity between brain regions during simple addition and number comparison. Specifically, native English speakers recruited more regions in left perisylvian regions, including Broca's area, whereas native Chinese speakers activated more premotor regions during the same task. Exactly which factors (for example, approach to reading and differences in learning strategies and education) bring about these differences in activation remains to be determined. With reference to the above discussion of the neural circuits that underlie symbolic number processing, it is of particular interest to note that cultural differences in brain function were even found for numerical-magnitude comparison of single-digit Arabic numerals¹⁰⁷. Together with studies from other cognitive domains^{108–110}, these findings reveal the striking transformative effect of cultural variability on brain function. Future studies should also take into account the way in which number words differ across languages and whether such differences influence the representation and processing of numerical magnitude in the brain.

Another pathway by which to investigate the influence of enculturation and education is to compare the neural activation that is associated with different methods and strategies for approaching mathematical problems. In one fMRI study¹¹¹, two groups of adult participants were asked to memorize prototypes of algebra problems in either a verbal format (for example, "Brian earns \$7 an hour and gets \$9 in tips.") or in a symbolic, equation format (for example, $7H + 9 = E$). During the acquisition of the fMRI data, participants were asked to calculate results using the information contained in the prototypes, by presenting them with problems such as 'hours = 3, earning = ?'. The two groups' behavioural performance was equivalent, but there were striking differences in the brain regions that were recruited during the problem solving. Specifically, participants in the 'verbal' group recruited left prefrontal regions, whereas those in the 'symbolic' group activated regions of the posterior parietal cortex.

In another study¹¹², fMRI was used to compare the neural correlates of solving algebraic problems by two methods that are taught in schools in Singapore: the 'symbol' method and the 'model' method. In the symbol method, children are taught to transform algebraic problems into symbolic equations, whereas in the model method they are taught to create diagrams that represent the information contained in the word problems. When adults were asked to use these methods to verify solutions to algebraic word problems, the two approaches

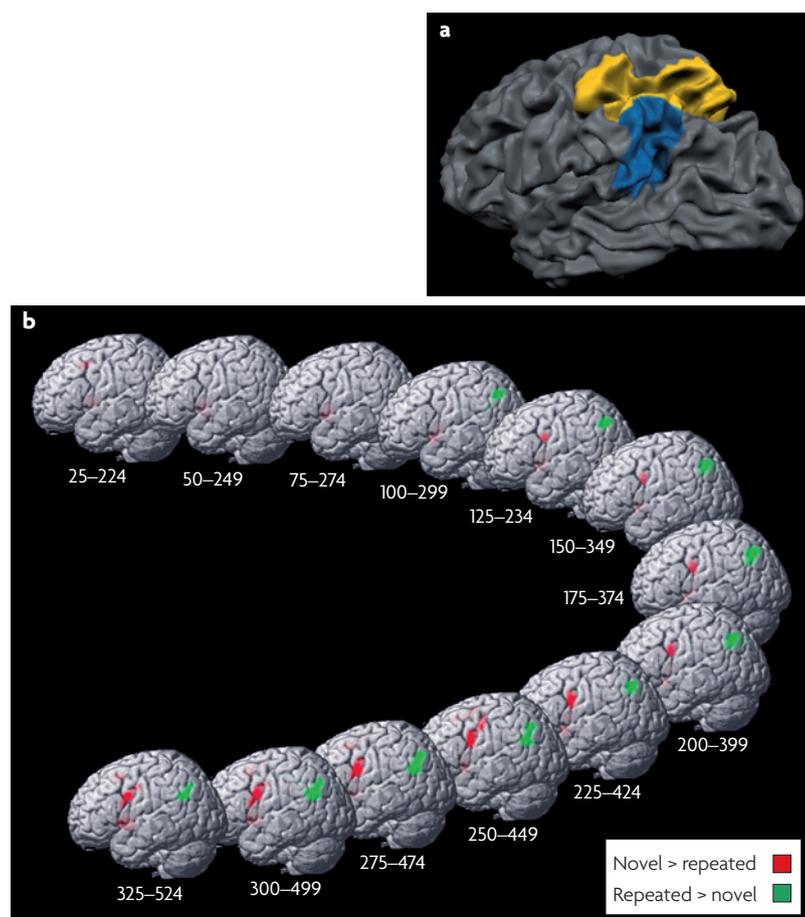


Figure 5 | The calculating brain changes dynamically as a function of learning.

a | Training for arithmetic problems leads to decreasing engagement of the inferior parietal cortex (shown in yellow) and increasing recruitment of the angular gyrus^{103–105} (shown in blue). Specifically, the left angular gyrus is more activated during the solving of trained than untrained problems. Furthermore, its relative activation is modulated by the type of instruction¹⁰⁴ and the type of arithmetic operation that is being learned¹⁰⁵.

b | During the learning of arithmetic problems, increases in the recruitment of the angular gyrus for repeated problems occur rapidly. The figure shows a moving time window of 200 scans (the scan ranges are indicated below the brain images) and reveals that there are significant changes in activity of the angular gyrus (shown in green) after only approximately 8 repetitions of a problem (corresponding to the time window between 100 and 299 scans), with increasing activation of this region for repeated compared with novel problems. In addition, an area in the left middle frontal gyrus (shown in red) was found to increase in its response to novel compared with repeated problems as a function of training. These findings suggest that the neural correlates of mental arithmetic rapidly undergo dynamic changes as a function of learning. Part **b** reproduced, with permission, from REF. 98 © (2007) Academic Press.

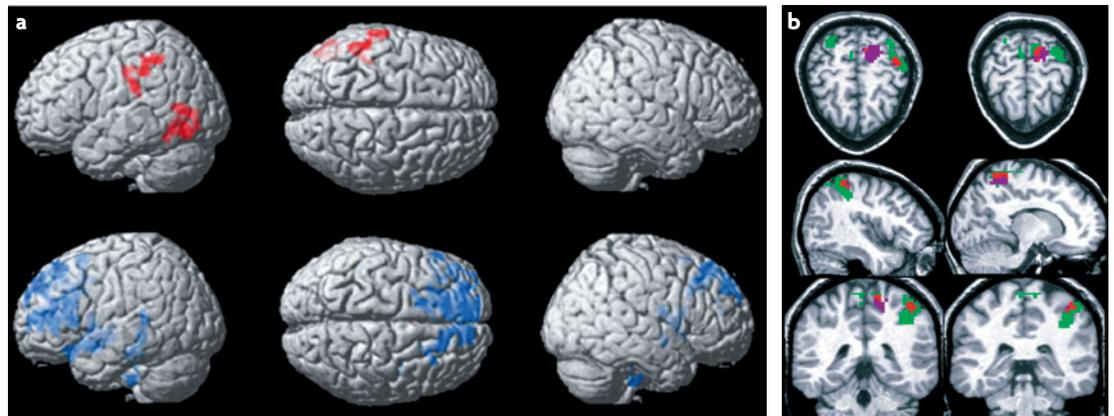


Figure 6 | Ontogenetic differences and similarities in the neural correlates of mental arithmetic and magnitude processing. **a** | Participants ranging from 8 to 19 years old were asked to verify the correctness of arithmetic equations (such as $5 + 3 = 9$) while brain activation was recorded using fMRI. Regions in red indicate areas in which activity during calculation increases with age. These included the left supramarginal gyrus, which has been shown to subserve adult calculation²⁹. Regions in blue indicate areas in which activation during calculation was negatively correlated with age. The engagement of frontal regions decreased as a function of age, perhaps reflecting increasing automaticity in the processing of arithmetic equations and less reliance on frontally mediated cognitive mechanisms. **b** | In an fMRI study¹¹⁴, 4-year-old children and adults were presented with trains of stimuli containing the same non-symbolic numerical magnitude (for example, 16 dots). Repetition of the numerical magnitude led to a decrease in the fMRI response of brain regions that encode numerical magnitude. Interspersed in the trains of repeated stimuli, stimuli that deviated in either numerical magnitude (for example, 32 dots instead of 16) or shape (for example, 16 squares instead of 16 dots) were presented. The presentation of deviants caused a recovery of the fMRI response. The intraparietal sulcus responded more to numerical-magnitude deviants in both 4-year-old children and adults. Regions of activation in adults are shown in green, regions of activation in children are shown in purple and the overlap in activation between children and adults is shown in red. Part **a** reproduced, with permission, from REF. 113 © (2005) Oxford University Press. Part **b** reproduced from REF. 115.

yielded equal behavioural performance but use of the symbol method was associated with greater activation of the superior parietal lobules and the precuneus. It is possible that the symbol method imposes greater attentional demands and thus is subjectively more difficult. In summary, recent data indicate that different instructional methods might result in different patterns of brain activation.

Neural correlates of number development

In a pioneering study, Rivera *et al.*¹¹³ revealed age-related increases in the recruitment of the left inferior parietal cortex (specifically the left SMG) during calculation in a cross-sectional sample of people aged between 8 and 19. As noted above, the SMG (together with other regions of the left temporoparietal cortex, such as the angular gyrus) is involved in mental arithmetic in adults. These developmental data therefore suggest that the adult outcome is the result of a process of developmental specialization of this region for mental arithmetic. Such developmental increases also occur in the left lateral occipito-temporal cortex, and they were coupled with reductions of activity in bilateral regions of the frontal cortex, the hippocampus and the basal ganglia¹¹³. Thus, a frontoparietal shift in activity (FIG. 6a) might underlie the development of arithmetic skills. The increase in the recruitment of the left SMG and the lateral occipitotemporal cortex suggests that there is an ontogenetic specialization of these regions for mental arithmetic and for the processing of symbolic visual stimuli, respectively. The decrease in the reliance on frontal regions might relate to reduced

reliance on processes of cognitive control, attention and working memory with age, whereas the decreases in the hippocampus suggest that there is increasing consolidation of arithmetic facts into long-term memory. These findings indicate that dynamic increases and decreases in activation occur in a large network of regions, again highlighting the importance of considering networks of activation rather than focusing on a select set of brain regions. Evidence for a frontoparietal shift has also been shown for more basic tasks such as symbolic^{28,74} and non-symbolic¹¹⁴ magnitude comparison: the modulation of IPS activation by numerical distance for both symbolic and non-symbolic magnitude comparisons increases with age^{28,115}. Taken together, the data suggest that although mental arithmetic leads to specialization of the left temporoparietal cortex, basic magnitude processing involves the ontogenetic specialization of the IPS.

Similar to monkeys⁷², children use more prefrontal regions during numerical processing than adults. This might suggest that the prefrontal cortex subserves the early association between external and internal representations of numerical magnitude in both non-human primates and human children. Importantly, however, there are also similarities between children and adults in the brain regions that underlie numerical-magnitude processing. One fMRI adaptation study investigated the neural correlates of numerical-magnitude representation in 4-year-old children and adults¹¹⁵. Participants were repeatedly presented with stimuli containing a particular number of dots (for example, 16). Interspersed into this train of repeated arrays of dots were stimuli containing

Cross-sectional experiments
Experiments that compare different groups of participants (for example, children of different ages) rather than longitudinally following individuals in a single group.

either different numerosities (for example, 32 dots) or the same numerical magnitude but different shapes (for example, squares instead of dots). Contrasting brain responses to number versus shape deviants revealed activation of the IPS (FIG. 6b) bilaterally in adults but in only the right IPS in 4-year-old children. Moreover, an ERP study¹¹⁶ in 3-month-old infants revealed sensitivity to numerical deviants in a right-lateralized frontoparietal network of regions.

Taken together, these findings indicate that learning and development result in the recruitment of distinct parietal circuits⁷³ for numerical-magnitude processing and calculation, with specialization of the left temporoparietal cortex for calculation and the bilateral IPS for numerical-magnitude processing. In future studies, the developmental changes that are associated with the learning of both symbolic-magnitude processing and arithmetic skills should be systematically studied within subjects to determine the relative independence of and interactions between the IPS and the left temporoparietal cortex in the development of these competencies. A developmental perspective of this nature will increase our understanding of how neural mechanisms for the representation and processing of numerical symbols emerge and how they are deployed to solve culturally invented problem-solving algorithms, such as mental arithmetic.

Conclusions and future directions

The study of the neural basis of numerical-magnitude processing provides a unique model of how basic representations and competencies that are thought to have a long evolutionary history interact with development, learning and enculturation to enable the use of culturally-invented mental tools, such as abstract numerical symbols.

Non-symbolic stimuli, like symbolic stimuli, are external representations of numerical magnitude that need to be mapped onto internal representations; the processes that enable such a mapping are not well understood. Current theories and computational models suggest^{67,78} that the acquisition of symbolic representations of numerical magnitude is grounded in the representations

of non-symbolic numerical magnitude. Alternatively, symbolic and non-symbolic external representations of numerical magnitude might be mapped onto different internal representations that have higher-order similarities, such as being ordered sequences, ultimately leading to similar activation patterns in the IPS^{57,58}.

Future empirical and computational modelling work should evaluate the extent to which qualitatively different representations of symbolic and non-symbolic numerical magnitude might exist and should determine how such representations are constructed during development. Rather than continuing to examine the common areas that are activated by symbolic and non-symbolic representations of numerical magnitude in children and adults, there is an urgent need for an understanding of the divergence of these representations. Studies that systematically compare the behavioural and neural changes that are associated with the developmental and learning trajectories of symbolic and non-symbolic magnitude processing can explore this divergence. In this vein, the role of extrastriate areas that are involved in specialization for the asemantic representation of visual symbols and of left-lateralized temporoparietal regions that are involved in symbolic representation of numerical magnitude should be systematically investigated.

A focus on children who are making the transition into the formal classroom would be particularly appropriate, as this represents a stage in development at which children are systematically (through formal education) introduced to symbolic representations of numerical magnitude. Cross-cultural studies will also help to increase our understanding of how cultural differences in symbolic representations of numerical magnitude (such as the difference in the way in which the teens are represented in the Chinese and English languages¹¹⁷) affect brain representations.

On a broader level, such investigations will provide a greater understanding of the mechanisms that allow cultural inventions to be represented and processed by the brain through both the recruitment of existing representation¹¹⁸ and the ontogenetic construction of new systems of representation.

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