Primer

Neural basis of mathematical cognition

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The human brain has remarkable capabilities for encoding and manipulating information about quantities. Understanding how the brain carries out such number and quantity is a problem not just for those interested in numerical cognition: it raises important questions that are relevant to understanding development, action, vision, language, executive function and cortical organisation. It is also a clear case of research into a core human psychological function having indisputable everyday relevance; hence the emphasis in early education on numeracy and later on mathematics.

The neural system for the arithmetical aspects of mathematics has its roots in the numerical capacities of ancestral species. There is evidence that we share with a wide variety of species a capacity to respond discriminatively to numerosities. This has been demonstrated in bees, fish, reptiles, birds, rodents, elephants, monkeys and apes. Electrophysiological recordings from monkey parietal cortex suggests that there are neurons in the lateral intraparietal cortex (LIP) that responds more the more objects are presented, and neurons in the fundus of the intraparietal sulcus (IPS) that are coarsely tuned to specific numerosities. That is, one neuron will respond more strongly to, say, four objects, but also, though less strongly, to three or five. These neurons are in areas in which neurons also response to space, time and object size and it has not been demonstrated that numerical responses are distinct from responses to these dimensions, and it has been suggested that these numerical responses are one of multiple duty responses that may be made by the same neurons.

Of course, there is much more to arithmetic than being able to recognise the numerosity of set of objects. Box 1 lists the numerical abilities expected of a nine year old in the UK. Even a relatively simple problem, one that a nine year old would be expected to know, such as multiplying 33 and 8 (33 x 8 = ?), requires a wide variety of cognitive processes. Minimally, it is necessary to know the meaning of the symbols 3, 8, x and =; to understand the procedure for two-digit multiplication; to retrieve the product of 8 and 3; and to add the products 8 x 3 and 8 x 30.

The IPS turns out to be part of the extensive network of brain areas that support human arithmetic (Figure 1). Like all networks it is distributed, and it is clear that numerical cognition engages perceptual, motor, spatial and mnemonic functions, but the hub areas are the parietal lobes that are activated in almost all numerical tasks. Depending on the task, and on the analytic criteria, activations are observed in the IPS on the left or the right or bilaterally.

Moreover, there appears to be a developmental trend from the right hemisphere to a bilateral representation, which may be related to a developmental linkage of the numerical processes to language. Interestingly, in adults, calculation appears to be in the same hemisphere as the primary language processing areas.

The first study of the neural basis of our number skills came from Henschen's original series of neurological patients in 1920s, and Gerstmann's early observations of the effects of damage to the part of the parietal lobe known as the left angular gyrus. It became clear that left parietal damage causes deficits in calculation, while damage to the left angular gyrus also disturbs the neural representation of fingers, additionally causing left–right confusion and agraphia. This tetrad of symptoms came to be known as 'Gerstmann's Syndrome', but the functional relationship between the symptoms is still unclear. The frontal lobes also play a role, and damage can disturb novel or complex tasks, but can leave routine calculations and simple fact retrieval intact.

Neuroimaging has confirmed and greatly elaborated the findings from neurological patients. It suggests that the IPS is the locus of core numerical processing. In particular, a wide range of tasks, using a variety of methodologies, the IPS is activated whenever numerical magnitude is implicated, even when the participant is unaware of the number through masking, or when the number is task-irrelevant. If the same numerosity is repeatedly presented, while other visual features are varied, activation in the area decreases. The IPS and surrounding regions also respond to tasks in which magnitudes such as time, size and velocity are analysed, and it has been suggested that numerical information emerges from a generalised magnitude system. There is some dispute about whether the IPS represents numerical magnitude abstractly or only tied to specific stimulus types — arrays of objects, digits or number words, for example 2, II, : and 'two'. There is evidence from conjunction analyses of neural activation that the same IPS area will respond to sets of objects distributed in time as well as in space (Figure 3), and to visual objects (squares) and auditory (tones). But there is some disputed evidence that IPS activity also adapts both to magnitude and to the format of the input — dots,

Box1.

National numeracy strategy: year 4 key objectives in numeracy.

- Use symbols correctly, including less than (<), greater than (>), equals (=)
- Round any positive integer less than 1000 to the nearest 10 or 100
- Recognise simple fractions that are several parts of a whole, and mixed numbers; recognise the equivalence of simple fractions
- Use known number facts and place value to add or subtract mentally, including any pair of two-digit whole numbers
- Carry out column addition and subtraction of two integers less than 1000, and column addition of more than two such integers
- Know by heart facts for the 2, 3, 4, 5 and 10 multiplication tables
- Derive quickly division facts corresponding to the 2, 3, 4, 5 and 10 multiplication tables. Find remainders after division
- Choose and use appropriate number operations and ways of calculating (mental, mental with jottings, pencil and paper) to solve problems

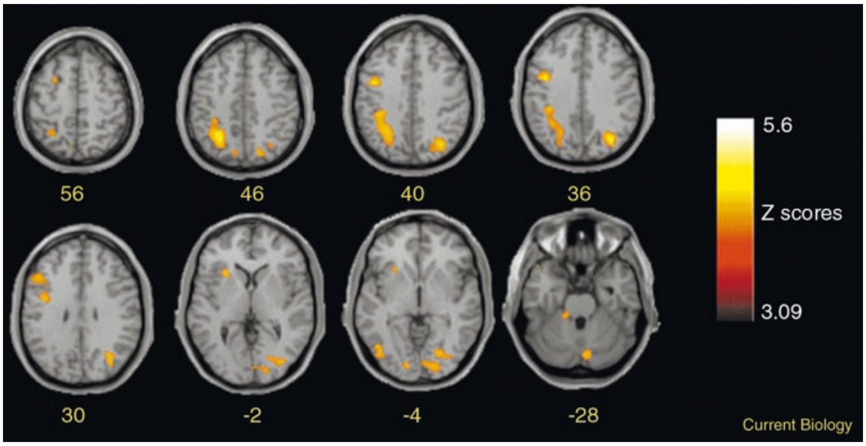

Figure 1. The extensive network deployed in retrieving arithmetical facts and using them in calculations.
Computing and retrieving task activations compared with a baseline of reading numbers (Adapted with permission from Zago *et al*.)

digits or words — suggesting multiple representations of number in this region.

Neuroimaging has also revealed, in the way that the study of neurological patients could only hint at, the neural changes effected by learning new arithmetical facts or procedures. So, for example, solving a new multiplication problem involves the IPS bilaterally, and also the frontal lobes, while dealing with the same problem a second time shifts the focus of activity to the angular gyrus in the left parietal lobes (Figure 2). This finding suggests that novel problems require the involvement of the IPS to represent the magnitude of the numbers in the problem, and the frontal control of goal-setting, working memory, and attention; while previously learned arithmetical facts appear to be accessed from memory via the angular gyrus. Thus for arithmetic, there appear to be two distinct circuits: the IPS bilaterally for tasks involving explicit representation of magnitude, such as subtraction, and the angular gyrus for the retrieval of previously learned facts.

Many numerate people, perhaps as many as 15%, automatically form a mental image of the sequence of numbers, called by Francis Galton, 'number forms', where the sequence is represented in two dimensions (and sometimes three-dimensions), usually embodying the decade boundaries and often a clock face for numbers to 12. There is now evidence that number forms have a distinct representation in the IPS bilaterally. Many more also have an unconscious spatial representation of numbers. Dehaene and colleagues, using a representational version of the stimulus-response compatibility paradigm, found that, with Western participants, small numbers were responded to faster with the left hand and large numbers faster with the right hand, suggesting that numbers are ordered small to large from left to right in representational space. The neural basis of this effect, involves not only the parietal lobe, but also frontal eye fields and right inferior frontal cortex. More generally, parietal and frontal lobe damage can cause neglect of space that in some patients is mirrored in a disturbance of their spatial representation of numbers.

Studies of the development of arithmetic suggest that children typically learn to calculate by manipulating objects in sets, combining sets of objects and partitioning sets of objects. Other studies show that children misunderstand number and make characteristic mistakes based on confusing other magnitudes with quantities. So it is reasonable to speculate that the IPS function for magnitude processing could be the core on which subsequent arithmetical development is founded. The capacity to compare larger numerosities has recently been found to correlate with arithmetical attainment though the causal connection is unclear.

A selective developmental disability in learning arithmetic, usually called dyscalculia, has been linked to an inability to mentally represent and manipulate numerosities, and to structural abnormalities in the IPS. Even very simple tasks, such as selecting the larger of two one-digit numbers can reveal abnormal activation in the in children with dyscalculia. Expert calculators, by contrast, also activate the typical parietal-frontal network, but also recruit other areas, including those associated with long-term and working memory to a greater extent when challenged with very difficult problems. There is some evidence

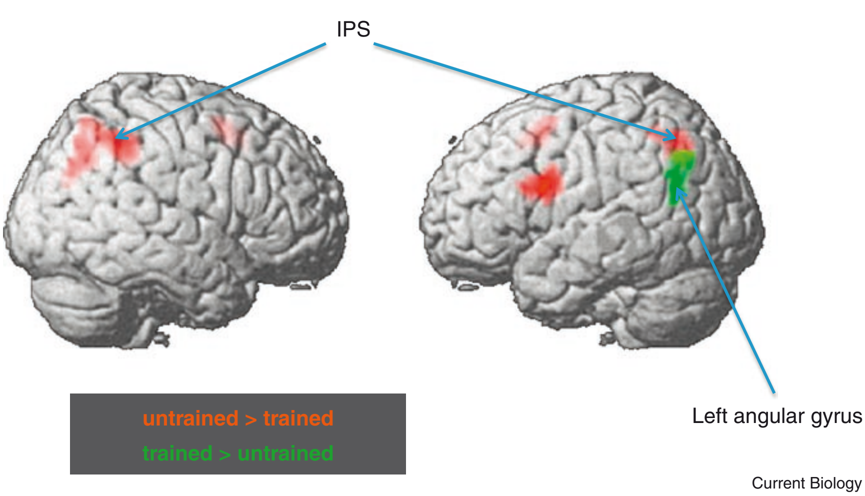

Figure 2. Learning new multiplication problems as compared with retrieving previously learned problems.
Left panels show extensive activation for novel problems in the IPS bilaterally and in the frontal lobes. The right panel shows greater activation in the left angular gyrus for previously learned problems (Adapted with permission from Ischebeck *et al*.).

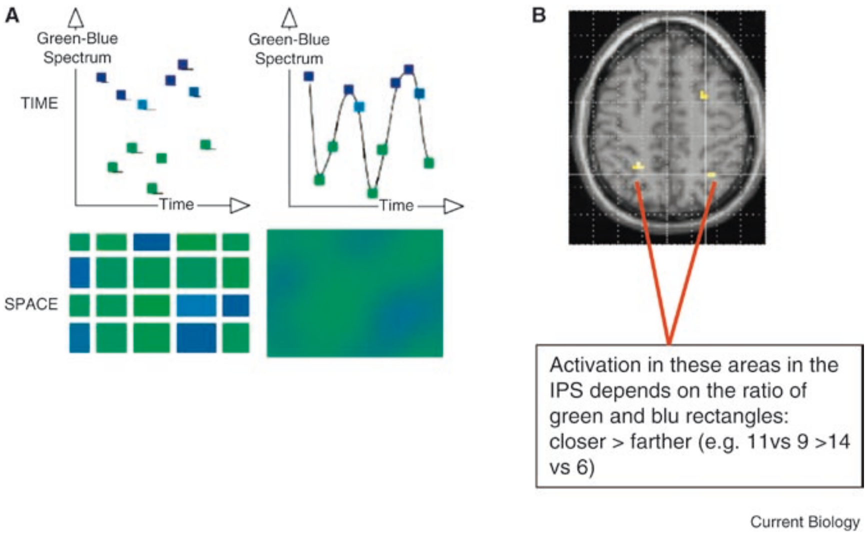

Figure 3. Numerosity processing in the IPS.
(A) Areas in the IPS bilaterally specific for numerosity processing whether the objects are distributed in space or in time . The task is to say whether there is more blue or more green, and activation in these areas is modulated by the ratio of blue to green rectangles with more activation the closer the ratio (B). (Adapted with permission from Castelli *et al*.)

that grey-matter density in the IPS of university mathematics teachers is correlated with their years of teaching, though, of course, it would be difficult to disentangle this from the effects of age that may also increase grey-matter density. Where simple number concepts end and more complex operations and concepts begin is a subject for future research. For example the link between time, space and numerical magnitudes extends to conceptual thinking and language analogous to perceptual and motor associations of these magnitudes.

Understanding the neural basis of mathematical processes could play an important role in improving mathematical education. This would help individuals struggling with to learn about numbers and arithmetic, such as dyscalculics, but it would also have a wider impact. Poor numeracy affects not only the life chance of individuals, it is a significant cost to society (about £2.4 billion per year in the UK, for example). Moreover, the level of mathematical competence in a society plays a causal role in its economic performance, as a recent OECD report demonstrates. However, for neuroscience to have a practical impact, we will need to know more about the neural networks underlying mathematical skills more complex than simple arithmetic, and in other areas of mathematics, including geometry and algebra.

Further reading

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