Photograph: Kevin Stearns.

deadline. My husband Sam Flaxman is also a young faculty on the tenure track and we are fortunate enough to be in the same department. Our schedule is highly orchestrated, down to a very fine scale. Surprises wreak havoc on our beautiful plans. Then, a sense of humor helps. I am lucky to be completely in love with my job and with my family, so the entire package is my lifestyle. But, there is not much room for anything else just now.

Do you have a 'scientific hero'? This is a timely question because one of my many scientific heroes has recently passed away. Thomas Eisner's office was just next door to the graduate student office that I occupied for nearly six years at Cornell. Tom was inspirational in so many ways — his love and understanding of natural history, his elegant way of unfolding a lecture, his insatiable curiosity. Tom was an elegant and creative experimentalist, an artist, and a true pioneer in integrating across disciplines. I have to also thank Tom for encouraging me to get back to creative writing. He edited a small piece I had written about the natural history of migration. I hope to someday get back to the writing, when the time is right. Thinking back, I also found great inspiration by many of my peers during graduate school. Winters in Ithaca can be dark and long. With so few distractions around, our social networks were very much intertwined with our research. For example, one of my first collaborators was an office mate with an impressive mathematical ability. So impressive that I agreed to marry him!

What are the big questions in your field? First, another question: what is my field? My group works at the interface of behavior, genetics, ecology, evolution and physiology, so I have a hard time sorting out how to define my field. Most of what I end up doing is tied to animal behavior. I think many of the big questions in behavior, evolution and ecology are related to technological advances and integration: advances in genomics and computational biology are opening up ways to look back in time — something evolutionary biologists are obsessed with. We are getting ever closer to understanding the molecular basis of phenotype and behavior — something that will enable a closer analysis of how evolution shapes phenotypic variation within and among populations and how populations split off from one another into separate species.

Finally, what advice would you give to those just entering your field of research? The job market is grim, getting funding is extremely competitive and publishing requires endurance and patience. If you love biology, however, then pursue it fully and I mean *fully*! Hard work does pay off and this can mean working hours that would look unreasonable to someone used to a 9 to 5 position. Embrace your career as your lifestyle rather than a job and do absolutely make sure you enjoy it (or at least, most of the time). Get out of your comfort zone, talk to a lot of people in and beyond your field, read widely and make time to let your mind wander. Keep a diary so you can track your ideas and goals for the present and future. Ask: what can I get done this term? This year? What is the next set of experiments now that I have this result? What would I love to be doing within the next five years? Be open to ideas that turn your world view upside down and inside out. Keep your eyes open — in the field or lab, when you are at a conference, or just walking to get a coffee.

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Primer

Neural basis of mathematical cognition

Brian Butterworth and Vincent Walsh

The human brain has remarkable capabilities for encoding and manipulating information about quantities. Understanding how the brain carries out such number and quantity processing 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 suggest that there are neurons in the lateral intraparietal cortex (LIP) that respond 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 respond to space, time and object size; 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

Box 1.

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

recognise the numerosity of a 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 the 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, for 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 input (tones). But there is some disputed evidence that IPS activity also adapts both to magnitude and to the format of the input — dots, digits or words — suggesting multiple representations of number in this region.

Neuroimaging has also revealed, in a 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

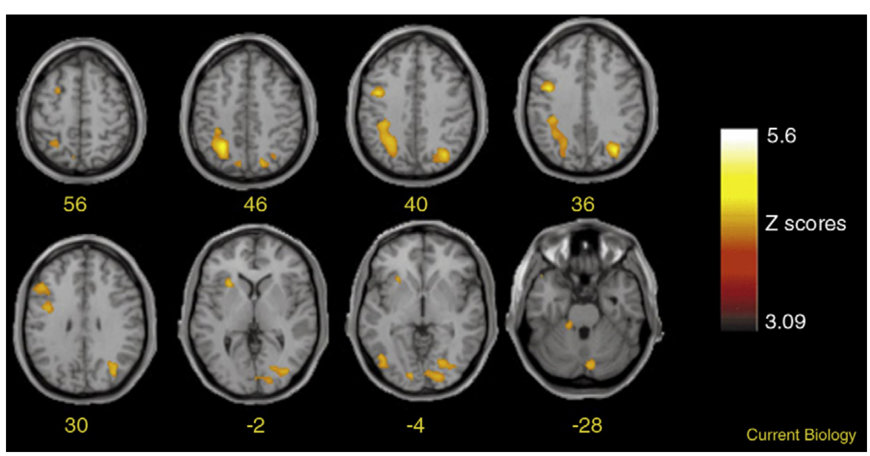

Figure 1. The extensive network deployed in retrieving arithmetical facts and using them in calculations.
Computing and retrieving task activations compared with a baseline of reading numbers. (Adapted with permission from Zago *et al*.)

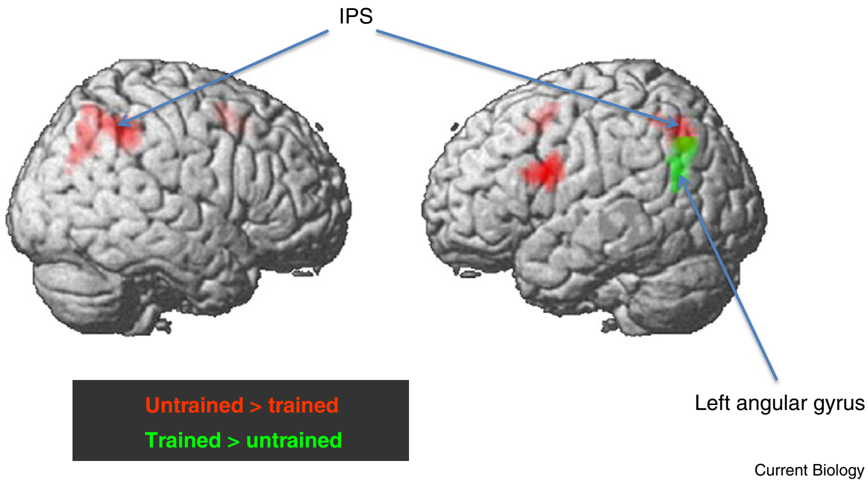

Figure 2. Learning new multiplication problems as compared with retrieving previously learned problems.
The left panel shows extensive activation for novel problems in the IPS bilaterally and in the frontal lobes. The right panel shows greater activation in the left angular gyrus for previously learned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

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 dam age can cause neglect of space that in some patients is mirrored in a disturbance of their spatial representation of numbers.

Studies on 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 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 that grey-matter density in the IPS of university mathematics teachers is correlated with their years of teaching, though, of course, it

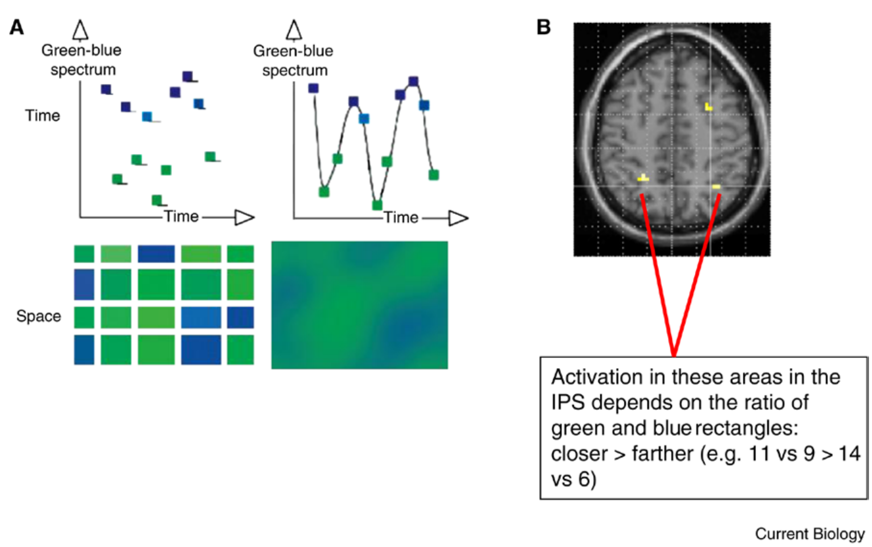

Figure 3. Numerosity processing in the IPS.
(A) Areas in the IPS bilaterally specific for numerosity processing whether the objects are distributed in space or in time. The task is to say whether there is more blue or more green, and activation in these areas is modulated by the ratio of blue to green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

would be difficult to disentangle this from the effects of age that may also increase grey-matter density.

Understanding the neural basis of mathematical processes could play an important role in improving mathematical education. This would help individuals struggling 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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Genetic detection of mislabeled fish from a certified sustainable fishery

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The decline and collapse of many of the world's fisheries has led to the implementation of social marketing that promotes the consumption of sustainably harvested seafood [1,2]. Because the success of this strategy depends on supply chain integrity, we investigated the accuracy of eco-labels for Patagonian toothfish, marketed as 'Chilean sea bass' (*Dissostichus eleginoides*), by genetically analyzing retail fish bearing certification labels from the Marine Stewardship Council (MSC). For Chilean sea bass, MSC certification labels indicate that fish were harvested from the only sustainable fishery [3,4], a population in waters surrounding the sub-Antarctic island of South Georgia and the nearby plateau at Shag Rocks [3]. We found that not all MSC-certified fish were Chilean sea bass from the certified stock: some were simply not *D. eleginoides,* but among those that were, we found significant genetic differences between the retail sample of fish and the certified stock population. Uncertified fish may not necessarily resemble stocks closest to their country of origin because capture and processing often occur at different places. However, significant differences between MSC-certified Chilean sea bass and the sole certified fishery for this species indicate that uncertified fish were inserted into the MSC supply chain.

Best known to consumers by its market name, 'Chilean sea bass', the Patagonian toothfish (*Dissostichus eleginoides*) is a slow-growing, long-lived species found primarily in the Southern Ocean surrounding Antarctica (Figure 1). Reported and unreported catches of *D. eleginoides* increased substantially in the 1990s [3,5] such that *D. eleginoides* is now regarded as overfished [3–6]. At present, the only fishery where this species is considered by the Marine Stewardship Council (MSC) as sustainably harvested is the South Georgia/Shag Rocks population (SGSR) fishery [3,4].

Our primary goal was to investigate supply-chain reliability for Chilean sea bass with respect to MSC certification. Although species substitutions (labeling less expensive species as more expensive species) are relatively easy to detect, resolving the geographic origin of samples within a single species requires genetic characterization of source populations. Therefore, we analyzed mitochondrial DNA (mtDNA) from retail-acquired fish using the same methods as a previous study [7] that revealed SGSR to be genetically highly distinct from populations north of the Antarctic Polar Front (APF), an oceanographic discontinuity separating the Southern Ocean from warmer water to the north (Figure 1). Briefly, we characterized fish by amplifying ~1200 nucleotides of mtDNA (control region flanked by tRNA proline and 12S rRNA) followed by digestion with a single restriction enzyme (*Bst*NI) and visualization with agarose electrophoresis (Supplemental information). Using the same method as the previous study [7] allowed us to compare retail MSC-certified fish to the only stock from which they could have been caught and validly labeled as MSC-certified. For comparison, we applied the same methods to a sample of uncertified fish, most of which were labeled with Chile as the country of origin.

We found that not all MSC-certified Chilean sea bass came from the certified fishery. A combination of PCR, *Bst*N1 digestion, and nucleotide sequencing showed that 8% (3 of 36) of fish labeled as MSC-certified Chilean sea bass were actually other species (Supplemental information). Among retail MSC-certified fish that were actually *D. eleginoides* (33 samples), 15% (5 of 33 samples) had mtDNA haplotypes not present in SGSR (haplotypes E, F, I, and J); haplotype B was found at an elevated frequency in the retail sample, and haplotypes C and D were not found in the retail sample (Figure 1). Overall, the haplotype content of retail certified *D. eleginoides* differed significantly from the SGSR stock (exact test for differentiation $P = 0.0026$; Supplemental information).

This discrepancy is likely caused by mislabeling of less desirable species and uncertified Chilean sea bass as MSC-certified Chilean sea bass at