Mid1p binding to the membrane is complex, as both amino- and carboxy-terminal fragments of mid1p can bind to the membrane independently, and both fragments also show self-interaction in immunoprecipitation experiments [16]. Thus, it seems possible that the oligomerization state of mid1p may be an important factor in regulating its distribution.

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Cognitive Training: Neural Correlates of Expert Skills

Expertise is a ubiquitous pre-requisite for modern life, but little is known about what neural mechanisms underpin the acquisition or employment of such skills. Recent evidence from functional magnetic imaging studies suggests that a network of frontal and parietal regions plays a crucial role.

Daniel Bor and Adrian M. Owen

Perhaps our most defining feature as a species is the ability to become experts in an array of mental tasks. While the skills of a champion chess player or professional musician are tremendous, many of us still show considerable expertise every day, such as whenever we use a computer or carry out various tasks at our workplace. Although much is known about the psychology of expertise, until recently there was a paucity of knowledge concerning what brain mechanisms give rise to such marked abilities. Three recent brain imaging studies have shed considerable light on this field [1–3]. These new data suggest that a network of regions comprising the lateral prefrontal cortex and posterior parietal cortex drive increased performance on tasks requiring memory skill, are critical for the use of such abilities, and dynamically co-ordinate a set of supporting regions to facilitate expertise.

One of the first studies to investigate the neural correlates of training and expertise was that of Olesen *et al.* [3]. Participants underwent training for five weeks on a battery of visual working memory tasks, and were scanned using functional magnetic resonance imaging (fMRI) before, during and after training. Consistent with previous studies [4], subjects not only improved significantly in their working memory capacity, but also on general cognitive tests that they had never trained on. As participants' working memory performance improved, the lateral prefrontal and posterior superior parietal cortex increased in activation. It was not clear, however, whether these regions were driving enhanced performance, or were simply working memory areas with more processing to carry out now that the subjects had increased in proficiency. Furthermore, the expertise of the participants was weak and of a very general nature, further limiting the conclusions of this research.

In their recent study, Moore *et al.* [2] examined expertise in a more specific way. Over the course of 10 days prior to scanning, participants were trained to become proficient at recognising one class of highly

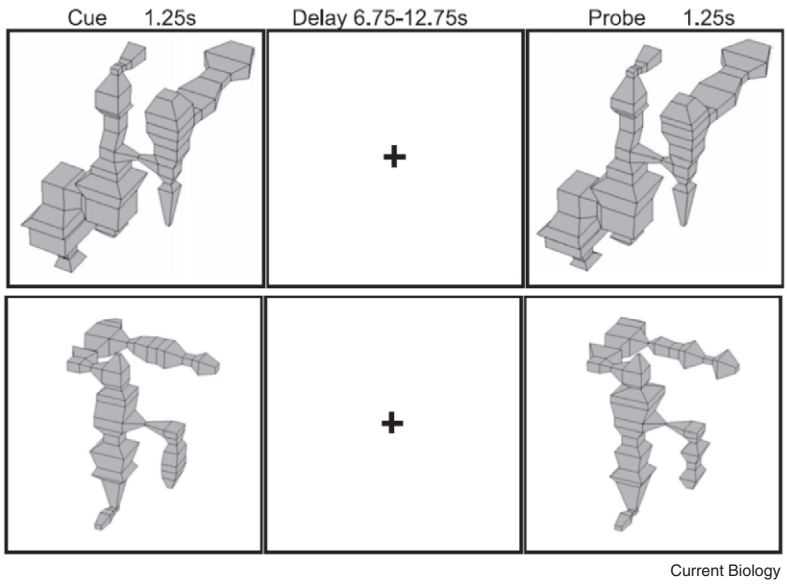

Figure 1. Stimuli used by Moore *et al.* [2].

Example trials from the working memory task performed during the fMRI scanning session. Participants were presented with one object, followed by a variable delay, before a second object was presented. Participants had to decide whether the second object was identical to the first. An example from each of the two classes of stimuli is shown.

complex abstract objects (see Figure 1). Immediately before fMRI scanning, participants were familiarised with six exemplars from an untrained class of objects. During scanning, each trial followed the same format: participants were presented with one object, followed by a variable delay, before a second object was presented. Participants had to decide whether the second object was identical to the first. There were three types of trial, involving novel stimuli from the trained class, novel stimuli from the untrained class, or familiar stimuli from the untrained class. The idea behind these three conditions was that any neural activity relating to the novel trained stimuli would reflect expertise-based processing, over and above the working memory and task-based components (the novel untrained stimuli) or any long-term memory components (the familiar untrained stimuli).

The fMRI results showed that the novel trained stimuli, compared with the non-trained conditions, elicited dorsolateral prefrontal and posterior parietal cortex activation, in very similar regions to that reported by Olesen *et al.* [3]. A further prominent activation, thought to reflect the long-term memory store of abstract visual objects, was found in occipitotemporal cortex. Interestingly, activity was strongest in dorsolateral prefrontal cortex and weakest in occipitotemporal cortex. Some time after scanning, expertise was assessed by examining discriminability between the trained objects in an upright or unfamiliar inverted orientation. Greater discriminability and thus a higher degree of expertise correlated with activity in the three regions activated in the main comparison above. These data, the authors suggest, paint a picture of a prefrontal–parietal network that increases in connectivity and strength as expertise develops, and enhances control and tuning of stimulus-specific regions, in this case occipitotemporal cortex.

While both of these studies [2,3] provide important clues about the neural correlates of expertise, the question remains as to the mechanism of learning, and of exactly how expertise is implemented. Both groups speculate that 'chunking' plays a key role in gaining expert skills. Chunking involves reorganizing information into familiar or regular structures and can sometimes improve memory performance substantially [5]. In many domains, including language acquisition and chess [6,7], chunking has been proposed as the major basis for increasing expertise.

Using a similar paradigm to that described by Moore *et al.* [2], we recently published an fMRI study that examined different forms of chunking [1], in the context of a series of investigations that examined chunking more generally [8–11]. Prior to scanning we taught participants 20 sets of four-digit sequences. During scanning, trials involved holding a novel eight digit sequence in short-term memory. One trial type involved purely random untrained sequences, another involved sequences where the first half included one trained sequence and the second half another, while a final trial type involved untrained, mathematically structured sequences (such as 28 39 50 61). We found that a very similar prefrontal–parietal network to that reported by Moore *et al.* [2] and Oleson *et al.* [3] was activated when the subjects could chunk the sequence according to the two trained halves. A medial parietal activation was also observed, which may reflect the long term memory store of digit sequences in a manner analogous to the occipitotemporal activation which was thought to represent the long-term store of abstract visual objects in the study by Moore *et al.* [2]. This activation pattern occurred when the trained stimuli trials were compared to the random sequence trials, thus controlling for the working memory and general task-based components, as well as when compared with a control task matched for retrieval of the digit chunks from long term memory, although in this case the medial parietal activation was not present.

These comparisons suggest a crucial role for the dorsolateral prefrontal and posterior parietal cortex in the utilisation of memory chunks, in order to optimise task performance during demanding conditions. Intriguingly, when the trials involving chunking according to the mathematical structure were compared with any of the random trials, the trained

sequence trials, or a control matched for level of mental arithmetic required, the prefrontal parietal network was still activated. This indicates that this network is more centrally involved in mathematical or logical based chunking strategies than in working memory, memory-based chunking, or mental arithmetic *per se*.

One striking aspect of these three studies is the consistency between them: all point to a network comprising dorsolateral prefrontal cortex and posterior parietal cortex as a general purpose expertise-based network. This network then coordinates activity in content specific regions, in order to retrieve and use the expertise acquired. While it is still unclear whether this network is actually involved in learning, the data from Moore *et al.* [2] that linked the extent of activation with the extent of expertise provide some evidence that this is the case. In addition, the nature of the expertise may well involve one the most powerful psychological mechanisms of human learning, that of chunking, as our own data suggest.

There are many questions still to be explored. For instance, are the same brain areas involved when expertise is more complex than simple memory? Both chess and music require the interplay of a range of processes, and it is an open question whether a more complex neural mechanism is required for them than for simple mnemonic content such as abstract shapes or digit sequences. Furthermore, if expertise involves increasing the ease with which one carries out a task, should this not lower brain activity in so called 'executive' areas, rather than raise it [12,13]? The relationship between level of activity in these regions and level of expertise seems far less straightforward than current theories suggest. Nevertheless, the studies outlined here have made important first steps in explaining the neural basis of expertise, and therefore how the human brain gives rise to the impressive range of skills we as humans possess.

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Genome Evolution: A Double Take for *Paramecium*

The surprising discovery of a whole-genome duplication in the otherwise compact genome of *Paramecium tetraurelia* displays the early forces driving gene retention and loss.

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Remnants of ancestral whole-genome duplications are evident in the genomes of many different species, including yeast, plants and fish [1–4]. The two-fold gene redundancy initially created by these events fades over time as, in subsequent generations, mutations accumulate in one gene copy or the other. In the case of very ancient whole-genome duplications, few of the duplicated genes remain in the descendants we see today. Aury and colleagues [5] have recently described the most completely preserved whole-genome duplication seen to date, in the genome of the ciliated protozoan *Paramecium tetraurelia*. The initial genome analysis must have left these researchers with a sense of double vision. Unlike the remnants of ancient whole-genome duplications described in other organisms, the majority of genes in *Paramecium* (68%) still have an obvious counterpart on a related chromosome, nestled between copies of the same neighboring genes (see the example in Figure 1A,B).

Immediately after a whole-genome duplication, there would seem to be little pressure for the cell to maintain two copies of each gene. The newly sequenced *Paramecium* genome, in which over half of duplicated genes still remain, provides an unprecedented glimpse into the principles that govern gene attrition following whole-genome duplication. The genes preferentially retained fall into three