kingdoms? Provocatively, several prion-like proteins have recently been shown to naturally form fibrils that could be beneficial, rather than aberrant, protein isoforms [20]. A broader perspective should promote a more complete understanding of the identities, functions, and relationships of the cytoskeletal superfamily.

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Working Memory: Linking Capacity with Selectivity

Working memory is one of the most intensively studied psychological processes, but little is known about what distinguishes individuals in their working memory capacity. Recent evidence from electroencephalogram recordings suggests that one crucial component of this variation is our ability to exclude irrelevant information.

Daniel Bor and Adrian M. Owen

While establishing links between mental processes and brain regions is undoubtedly important, these results alone tell us little about the psychological mechanisms under study. Neuroimaging, however, has the potential to inform us about psychology as well as neurophysiology. Indeed, it is possible under certain circumstances for neuroimaging to provide a more sensitive measure of psychological mechanisms than cruder behavioural scores can supply. Vogel *et al*. [1] have recently provided an elegant and striking example of this, by using electroencephalogram (EEG) data to link poor working memory performance with the unnecesary retention of irrelevant items.

Despite a plethora of neuroimaging and behavioural studies, comparatively little is known about how we retain information in working memory [2,3]. In the last year, however, three neuroimaging papers [1,4,5] have reported studies which shed light on how the brain supports this process by using novel approaches to index working memory storage capacity. Using functional magnetic resonance imaging (fMRI), Todd and Marois [4] found that activity in the posterior parietal cortex reflected the number of visual items a volunteer was able to retain in working memory. In a related study, Vogel and Machizawa [5] presented subjects with varying numbers of visual stimuli to one half of their visual field. EEG recordings in parietal and occipital cortices showed greater activity in the hemisphere opposite to the attended stimuli, compared to the hemisphere on the same side. Moreover, this difference varied with the number of items that were successfully encoded. They labelled this novel index of working memory storage 'contralateral delay activity'. Further analyses demonstrated that the contralateral delay activity associated with the increase from two to four items was highly correlated with working memory capacity between subjects. In other words, two items consumed a larger proportion of working memory storage capacity for subjects with poorer working memory.

Most recently, Vogel *et al*. [1] extended this approach by examining what happens when some of the items in an array are targets to be retained in working memory, while others are distractors to be ignored. As before, only items on one side of the visual field were attended to, in order to measure the contralateral delay activity. Subjects had to remember either two or four red items in the cued visual field for one second, with half of the two red item trials including two blue distractors to be ignored. For volunteers with a high working memory capacity, the amplitude of the contralateral delay activity for trials including two targets and two distractors was very similar to when they only saw two targets. In other words, this group were effectively keeping irrelevant objects from being stored unnecessarily in working memory. In striking contrast, however, in the volunteers with a low working memory capacity, the amplitude of the contralateral delay activity for the trials with two targets and two distractors was almost identical to that for the trials with four targets. In other words, the low capacity group were almost completely ineffective at keeping distractors from entering working memory. In order to test this relationship more formally, Vogel *et al*. [1] used a measure of filtering efficiency, based on the contralateral delay activity ratio between the trials with two targets alone and the trials with two targets and two distractors. Again, they found that filtering efficiency was highly correlated with memory capacity.

One explanation for these results is that the filtering task is just too difficult for low capacity subjects, as colour is known to be especially resistant to selection in this way. To rule out this possibility, Vogel *et al*. [1] ran a second experiment in which subjects had to filter out irrelevant items based on their location, a much simpler stimulus property. Similar results were found, confirming that low capacity individuals are generally impaired at keeping irrelevant items out of working memory.

One final question addressed in this study was whether low capacity individuals are generally impaired at exerting effective control over any aspect of working memory, or specifically impaired at excluding irrelevant information. In a third experiment, Vogel *et al*. [1] introduced a second stage of presentation in which additional targets or additional distractors were presented. Although all volunteers had no trouble adding additional targets to working memory, the low working memory capacity volunteers alone added the additional distractors, just as if they were targets. This result shows that the low working memory capacity subjects were able to control working memory items in sophisticated ways when it came to adding additional targets, but they were selectively impaired at filtering out distractors.

On the basis of these experiments, Vogel *et al*. [1] concluded that working memory capacity is partly determined by the efficiency with which irrelevant items are excluded. It is worth noting, however, that no causal link between working memory filtering efficiency and capacity has actually been established. Indeed, it is quite possible that both indices correlate simply because they share an underlying process, such as attentional control. Patient data are usually required to establish unequivocally that such links exist and a number of recent studies have sought to address this problem.

Peers *et al*. [6], for example, measured behavioural short term memory filtering efficiency and working memory capacity in healthy controls and in patients with frontal-lobe or parietal-lobe lesions. In contrast to the results from Vogel *et al*. [1], they found no relationship between these scores. Moreover, although capacity deficits were indeed associated with damage to the parietal cortex (specifically the temporoparietal junction), consistent with recent imaging studies [1,4,5], they were behaviourally associated with processing speed, rather than filtering efficiency. Filtering efficiency itself was predicted only by lesion volume, regardless of whether that lesion was in the frontal or parietal lobe. It is possible that such relationships are more easily measured using neurophysiological methods than behavioural measures alone and further studies are clearly needed to resolve this apparent inconsistency.

Although these recent papers [1,4–6] clearly implicate the parietal cortex in working memory storage, many working memory processes have traditionally been linked with more anterior regions of the brain. For example, regions of the lateral prefrontal cortex have been associated with working memory processing through numerous monkey electrophysiological studies [7], human neuroimaging studies [8], and more recently through investigations in patients with damage to the frontal lobe [9]. One possibility, as Vogel *et al*. [1] suggest, is that the prefrontal cortex is responsible for executive control functions that are required for working memory, such as biasing the parietal cortex in ways that determine which working memory items are actually selected for storage. On the other hand, Dehaene *et al*. [10] have suggested that the lateral prefrontal and posterior parietal cortices form a tight network which supports a ‘global workspace’ capable of mediating any effortful task, including those tasks that require working memory.

Despite these unresolved issues, Vogel *et al*. [1] have expanded our view of the machinery of working memory; specifically, how individuals differ in their working memory capacity and how this may relate to activity in posterior association areas of the brain such as the parietal lobe. In this sense, the study adds to the growing number of investigations that have suggested that working memory is a more complex psychological concept than previously assumed. For example, while Vogel *et al*. [1] have intimated that working memory performance can be impaired by storing irrelevant items, other recent studies have shown that working memory performance can be enhanced by recoding relevant items into a more efficient form, at times dramatically so [11], and have also linked such working memory modulation to changes of activity in prefrontal and parietal cortices [12,13]. If, as has been suggested [14], working memory capacity is one of the key components of intelligence, there may well be further surprises down the road before we come to a model sophisticated enough to help explain humanity's greatest achievements.

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