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Working Memory: Imaging the Magic Number Four

Dispatch

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Many brain regions have been implicated in memory performance, but the relationship between memory capacity and neural activity has not been clear. Recent studies show that activity in the posterior parietal cortex increases with working memory load, implicating this region in the storage of representations in visual memory.

Working memory has been described in various ways: as a cognitive system for both the temporary storage and manipulation of remembered information [1,2]; as the type of memory that is active and only relevant for a short period of time [3,4]; and as the specific process by which a remembered stimulus is held 'on-line' to guide behaviour in the absence of external cues or prompts [5]. While definitions vary, few disagree that working memory capacity refers to the number of items of information that can maintained over a short delay interval and contributes to performance on a wide variety of cognitive tasks, from complex decision making to selective attention and language [1].

In spite of this, a precise neurophysiological correlate of working memory storage capacity has not previously been identified. A common assumption in both electrophysiological recording studies in monkeys and functional neuroimaging studies in humans is that activity that is sustained during a delay period reflects maintenance or storage processes, and may therefore provide a key to the neural basis of known limits on storage capacity. For example, several early single-unit recording studies revealed sustained neuronal firing in the lateral frontal cortex of monkeys during the retention interval of delayed response tasks [6,7], suggesting the temporary storage of some aspect of the stimulus to be remembered. But visual-form-specific neurons with activity that is sustained during a delay have also been found in area TE and in perirhinal cortex in the anterior temporal lobe [8,9], while delay-dependent spatial working memory neurons have been identified in the parietal cortex [10].

In humans, several event-related functional magnetic resonance imaging (fMRI) studies [11–13] have also found persistent frontal-lobe activity during retention intervals of delayed response tasks. But some of these studies have failed to show a relationship between frontal activity and memory load in such tasks, arguing against a role for this region in basic storage processes [13]. Moreover, sustained activity during delays, broadly similar to that observed in the frontal-lobe, has also been reported in other cortical regions, such as the dorsal premotor and posterior parietal cortices [14].

The question that arises, therefore, is whether working memory storage can in fact be localised at all, or whether it is simply a general property of a distributed neural system. Two recent studies [15,16] have shed light on this issue by identifying, for the first time, neurophysiological correlates of working memory capacity in humans. Vogel and Machizawa [15] recorded event-related potentials (ERPs) from healthy young adults while they performed a simple visual memory task. On each trial, an array of coloured squares was presented for 100 milliseconds and the volunteers were required to remember the items in one hemifield. Memory was tested one second later by presenting a test array that was either identical to the remembered array or differed by one colour.

Beginning approximately 200 milliseconds after the onset of the memory array and persisting throughout the retention interval, a large negative voltage was observed over posterior parietal and lateral occipital electrode sites in the hemisphere contralateral to the remembered items. Moreover, increasing the number of items in the memory array between one and three squares increased the size of the observed effect, consistent with the notion that amplitude is sensitive to the number of representations that are being held in visual working memory. In contrast, when the array size was increased beyond normal memory capacity — approximately three items — to six, eight and ten items per side, there was no significant increase in amplitude.

This provides a further indication that delay activity reflects the specific maintenance of representations in visual memory, reaching a limit at approximately four items. Indeed, a significant limitation of previous neurophysiological studies that have reported memory load effects has been that the amount of activity continues to increase for loads that exceed memory capacity [11,17], suggesting that these measures reflect the contribution of other, less fundamental, mnemonic processes such as increased executive processing, arousal or general effort.

The new findings of Vogel and Machizawa [15] demonstrate, for the first time, a direct relationship between neural activity and memory capacity, although given the limited spatial resolution of ERPs the precise neural locus of this relationship is less clear. Todd and Marois [16] have recently addressed this issue using event-related fMRI and a similar behavioural paradigm. Healthy volunteers were presented with a sample display of between one and eight coloured disks, and following a 1200 milliseconds delay were required to decide whether a probe disk matched one of the sample disks in both colour and location.

As in the other new study, Todd and Marois [16] found that performance declined with increasing set size, levelling off at between three and four items when visual memory capacity was reached. The imaging data

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revealed that activity within a single bilaterally symmetric region of the intraparietal and intraoccipital sulci correlated with the number of objects encoded, reaching a plateau by set size four. Crucially, the general effects of task difficulty could be ruled out because, beyond set size four, accuracy decreased and reaction times increased, yet activity in this region remained constant, as did the number of items successfully encoded.

In a subsequent experiment, a longer, 9200 millisecond retention interval was used to examine separately whether the observed load-dependent activity was related to the encoding, maintenance or retrieval of information. The intraparietal and intraoccipital sulci were more active at larger set sizes during both encoding and maintenance, but not during retrieval. These results strongly suggest that the posterior parietal cortex acts as a capacity-limited store for the representation of visual information. Moreover, no such relationship was demonstrated for any lateral frontal-lobe region, even when significance thresholds were relaxed tenfold.

These two studies [15,16] are entirely consistent with those working memory models that have assumed that storage of information occurs in posterior cortical association areas, including the parietal cortex, while the frontal-lobe contribution is via various ‘top-down’ executive processes on those stored representations [2,18,19]. According to such models, sustained frontal-lobe activity does not reflect storage *per se*, but rather, operations such as active rehearsal and strategic encoding (‘chunking’, for example) that are essential for maintaining a stored representation across prolonged and/or interrupted delays and when storage demands exceed capacity. In fact, recent fMRI studies have suggested that, under certain circumstances, frontal-lobe activity may be entirely dissociated from basic storage demands. For example, where the information to be remembered can be strategically recoded through chunking, frontal-lobe activity has been shown to increase, while working memory demand effectively decreases [20].

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