

Processes of Working Memory in Mind and Brain

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ABSTRACT—*Working memory is often conceptualized as storage buffers that retain information briefly, rehearsal processes that refresh the buffers, and executive processes that manipulate the contents of the buffers. We review evidence about the brain mechanisms that may underlie storage and rehearsal in working memory. We hypothesize that storage is mediated by the same brain structures that process perceptual information and that rehearsal engages a network of brain areas that also controls attention to external stimuli.*

KEYWORDS—*working memory; neuroimaging; storage; rehearsal*

Multiply 68×7 in your head.

How did you perform this task? You might have first multiplied 8×7 , noted that the answer is 56, carried the 5, multiplied 6×7 to yield 42, added the carried 5 to get 47, and then answered 476. Working memory is engaged by this task and others that require the brief storage and manipulation of information in the service of some goal. Working memory is a system that can store a small amount of information briefly, keeping that information quickly accessible and available for transformation by rules and strategies, while updating it frequently. Without working memory, people would not be able to reason, solve problems, speak and understand language, and engage in other activities associated with intelligent life.

WORKING MEMORY IN THE MIND

How is working memory organized? Although psychologists know a good deal about the characteristics of working memory (e.g., that it has limited storage capacity and limited duration), there is as yet no consensus about a model of its processes.

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According to one popular model proposed by Baddeley (2001), working memory consists of buffers, each of which is responsible for storing information in some code. There is one buffer responsible for storing verbal information, one for visual or spatial information, and one for episodes, regardless of the modality of coding. The model further postulates that there are “rehearsal” processes that refresh the information in storage and keep it accessible. Each of the buffers articulates with long-term memory, so information can enter working memory either from the outside world or from the contents of long-term memory. Finally, this model includes executive processes that manipulate information in the buffers in the service of complex cognition, such as mental arithmetic.

Research that has been guided by this model has concentrated on clarifying the characteristics of the storage buffers, rehearsal processes, and executive processes. We forgo further discussion of executive processes here in light of recent reviews of this topic (e.g., Smith & Jonides, 1999). Instead, we focus on what brain research has shown about the neural underpinnings of storage and rehearsal.

WORKING MEMORY IN THE BRAIN

Let us summarize our hypothesis before providing detail. Accumulating evidence suggests that storage and rehearsal in working memory are accomplished by mechanisms that have evolved to work on problems of perception and action. With respect to storage, we claim that the same brain regions that are involved in encoding information are those that are maintained in a temporarily active state while that information is retained for short intervals. That is, these same areas mediate working memory. Most often, this encoding occurs via posterior brain mechanisms (e.g., in temporal and parietal cortex), although sometimes this encoding can represent not input, but prospective output in anterior cortex, as in the motor code that may be used to represent speech sounds or action. With respect to rehearsal, we claim that the attentional mechanisms that are used to refresh internal representations in working memory are just the ones used to modulate sensory processing when

information enters the senses. These mechanisms make use of both the perceptual and the motor systems.

Brain Mechanisms of Storage

Where is information stored in working memory? A partial answer to this question comes from studies in which lesions are made to lateral parts of the frontal cortex in monkeys. These lesions yield a deficit in these animals when they perform a spatial delayed-response task. In this task, a marker appears in the animals' visual field, and they must remember the position of this marker for several seconds (a retention interval) after it disappears, until a cue is given for them to shift their gaze to this position. The results from such experiments have been elaborated by recording the activity of single neurons in the same regions of frontal cortex; some of these neurons are active during the retention interval in these tasks, but not when the position is first marked and not when the monkey is responding with an eye movement after the retention interval (see, e.g., Goldman-Rakic, 1987). Moreover, there is evidence that single cells in parietal cortex are also responsive during the retention interval of a spatial delayed-response task (e.g., Chafee & Goldman-Rakic, 1998), and that single cells in inferior temporal cortex are responsive during a delayed-response task using objects, rather than spatial positions, as stimuli (e.g., Miller & Desimone, 1994). So, lateral frontal cortex is not unique in its responsiveness to retained stimuli. What, then, are the respective roles of posterior and anterior cortex for retention in working memory?

Malmö (1942) noted that the delayed-response deficit in monkeys with frontal lesions was restricted to performance in a lighted environment. When the delayed-response task was given to the animals in a darkened room, they did not show deficits in performance. This raises the possibility that the function of frontal versus posterior cortex in working memory may differ depending on the presence of interference during the memory task. In the light, the animals may have been distracted; perhaps their performance suffered because their lesions impaired frontal mechanisms that fight distraction. Confirming this observation in a task requiring that objects be remembered, Miller and Desimone (1994) found that the retention-interval activity of single cells in inferior temporal cortex was dampened by distraction, but the activity of cells in lateral frontal cortex was not. A parallel result for spatial memory has been documented in superior parietal cortex versus frontal cortex.

What is interesting about the posterior sites of activation in these studies is that they correspond nicely to the sites that are activated during perception: The pathway that processes spatial information, the *dorsal pathway*, is in parietal cortex, and the pathway that processes information about object identity, the *ventral pathway*, is in temporal cortex. Thus, these studies of working memory in monkeys lead to the view that a critical way

station for storage in working memory is posterior cortex, and that the posterior sites crucial for working memory map onto the sites used for perceptual functions.

This hypothesis receives support from studies of patients with brain lesions that result in working memory deficits. Verbal working memory deficits result from posterior lesions, principally in the left posterior cortex (e.g., Shallice & Warrington, 1970), and lesions of right posterior cortex result in deficits in spatial working memory (e.g., Hanley, Young, & Pearson, 1991). Thus, it appears that posterior cortex may be more important than frontal cortex for the storage of information in working memory.

D'Esposito and Postle's (1999) review of 11 studies of patients with frontal lesions confirms this idea. These patients showed no deficits in verbal and spatial span tasks (tasks in which people are given a number of verbal items or spatial locations to remember and recall in order). There are also data suggesting that posterior lesions in the region of parietal and temporal cortex do yield deficits in these tasks, although these data are limited. D'Esposito and Postle also found that patients with frontal lesions were more likely to show deficits on delayed-response tasks when the retention interval included distracting stimulation than when no distraction occurred. Thus, there is a convergence of evidence from studies of monkeys and humans with brain damage: The involvement of frontal cortex appears to be important in storage when there is interference from other stimulation during a retention interval. Otherwise, posterior cortex may be the first site of working memory storage.

We argue that the sites of storage in posterior cortex may be the sites at which information is encoded in the first place. Perhaps the best evidence for this claim comes from the distinction between the dorsal and ventral streams for visual processing. As we noted earlier, single-cell recordings in monkeys show delay-sensitive activity in neurons of parietal cortex for spatial stimuli and in neurons of temporal cortex for objects. Neuroimaging studies of the storage of spatial and visual stimuli in humans are consistent with this pattern in that activations associated with spatial storage occur in dorsal parietal cortex, whereas activations associated with object storage occur in ventral temporal cortex (Wager & Smith, 2003). Taken together, these results suggest a parallel between the perceptual mechanisms that encode spatial and visual stimuli and the mechanisms that store representations of these stimuli in working memory. A similar case can be made for the mechanisms that encode speech and those that store verbal material in working memory, although the mechanisms involved in this storage appear to recruit posterior and inferior frontal cortex. All in all, though, the available evidence on storage in working memory in general is consistent with the hypothesis that storage recapitulates perception. If this is so, then one would predict that rehearsal of stored material might use machinery that is used to keep stored representations active. We review evidence about this hypothesis next.

Brain Mechanisms of Rehearsal

Perceptual systems continually build new representations of the environment from an ever-changing stream of sensory input (e.g., visible light, sound waves). The resulting perceptions are transient, and it is this transience that allows perceptual experience to be continuous over time. But a perception is not the same as a working memory. Perceptions are updated and replaced continuously, whereas memories need to be static and unchanging for the storage duration. So, there is an inherent conflict between the adaptive “forgetfulness” of the perceptual systems and the desired “retentiveness” of working memory, even in the face of the evidence we reviewed suggesting common brain mechanisms for the two. How do we reconcile this conflict? One possibility is that the perceptual systems have built into them a brief memory for information even after direct stimulation ceases. Research on very brief visual and auditory memories suggests that this is a plausible view. But the retention periods afforded by the perceptual systems alone are too short to be of much use in more complex cognitive activities of the sort that use working memory. For example, a telephone caller might easily spend several seconds between finding a number in a phone book and dialing that number, and such a delay well outlasts any perceptual activation that attends encoding the digits from the phone book. If the perceptual machinery is used for working memory, in short, there must be a mechanism to get the “forgetful” perceptual systems to remember. One solution is to remind them over and over again by applying attention to the stored representations and rehearsing these representations.

The specific processes of rehearsal differ depending on the type of information stored, whether visual, spatial, or verbal. As a case study, we focus here on spatial working memory. Imagine that you are performing a typical delayed-response task used to assess spatial working memory. You fixate your gaze at the center of a computer display and keep it there throughout. Suddenly, a character is flashed somewhere on the display. A few seconds pass, and a second character (referred to as a probe) appears. Your task is to specify whether its location is the same as the location of the character you observed originally. Obviously, this task requires keeping active a stored representation of the location during the delay. If rehearsal is involved in keeping this representation active, what exactly are you rehearsing?

There is evidence that stored representations of spatial information are mediated by activation of an area in the occipital lobe called extrastriate cortex (Jonides et al., 1993). An important characteristic of extrastriate cortex is its topographical organization, whereby adjacent locations in external space are represented in adjacent brain areas. Thus, the spatial integrity of the display used in a spatial delayed-response task may be preserved in spatial working memory. If so, rehearsing locations in working memory may be analogous to shifting attention to perceived locations in physical space. In humans, such shifts of

attention are accomplished either by moving the eyes or by covertly moving attention without eye movements. This view, then, treats spatial rehearsal of working memory representations as a case of shifting attention in the same way one would when viewing visual stimuli.

Consider the following pair of experiments (reviewed by Awh & Jonides, 2001). In one, subjects performed a spatial delayed-response task in which the location of a single letter had to be remembered until a probe appeared. During the retention interval, a shape appeared, and subjects indicated which shape it was with a key press. On some trials the shapes appeared in the target location, and on other trials they appeared in other locations. If attention was directed toward the target location in working memory, then there should have been improved visual processing of a shape at that location, a benefit of spatial attention. Indeed, this was so. But this benefit did not accrue if the subjects had to remember the identity of the letter rather than its location. A later experiment showed further that having subjects shift their attention away from a to-be-remembered target location during a retention interval harmed their memory for that location. These results indicate that the same mechanism that mediates shifts of attention also plays a role in the rehearsal of spatial information.

What is this mechanism? In a review of studies of selective attention to visual perceptual stimuli, Kastner and Ungerleider (2000) documented a network that includes regions in superior parietal and frontal cortex. Given that shifting of spatial attention occurs both during rehearsal of working memory representations and in perception of visual scenes, it is tempting to conclude that the regions identified by Kastner and Ungerleider are also involved in working memory. Although it is possible that different brain areas implement spatial attention in these two kinds of processing, neuroimaging data show that the same network of frontal and parietal brain areas is activated during many different types of spatial attention and spatial working memory tasks. This provides another layer of evidence that the source of spatial attention is the same in working memory and perception. The site on which this attentional mechanism exerts its effect is extrastriate cortex, presumably where the spatial information is stored (Awh et al., 1999).

A Working Hypothesis

We propose, then, that the storage and rehearsal of information in working memory goes like this: Information entering working memory from the visual external world is processed by structures in the parietal and temporal lobes specialized for perceptual processing, and it is these same structures that remain active when the stimulus is removed for a brief duration. That is, working memory storage uses the mechanisms that underlie perception. Likewise, information entering working memory from long-term memory also is stored via the structures that mediated its perception (see, e.g., Kosslyn, Thompson, Kim,

& Alpert, 1995). The activation in these structures will fade with time and interference unless there is a repeated upward modulation of them, and this modulation (rehearsal) is controlled by the circuitry that also controls modulation of incoming information (i.e., selective attention mechanisms). The circuitry that controls rehearsal makes use of perceptual-motor processes in parietal and frontal cortex, including the same frontal mechanisms that control external speech.

Of course, this hypothesis needs much work to be tested thoroughly. Is there storage that does not recruit perceptual mechanisms? Are there components of rehearsal that may not recruit the attentional system? Are the parts of parietal and frontal cortex that are recruited by rehearsal really identical to those that mediate the allocation of attention to stimuli in the world? Are the mechanisms of working memory in the face of distraction different from those responsible for working memory when there is no distraction present, and do these two cases involve the perceptual systems differently? These are questions whose answers may lead to disconfirmation of the hypothesis. At present, though, it appears sensible to entertain the hypothesis that working memory is possible because of a harnessing of processes that evolved for perceptual purposes.

Recommended Reading

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