Working memory as a mental workspace: Why activated long-term memory is not enough

cortex participate in perception of light and dark, orientation, and so on. Although it seems straightforward that retaining information in working memory about a fixation dot, or the location of a saccade target, may involve activation of regions that participated in its perception, it is less clear that this is an activated long-term memory. Suppose subjects are presented with a novel shape to remember. It could be argued that elements of the shape (corners, curves, etc.) are retained by invoking neural representations of these features learned over time, thus perhaps constituting long-term memories bound in the current episode into the novel shape. In the case of five novel shapes, of different colors, the argument could be similarly made that the content of working memory is a binding of long-term memories. It seems, however, that there is a meaningful sense in which the "content" of working memory is more a binding of features to constitute a new representation than it is activated long-term memories. In the same vein, the proposition "John loves Mary" is distinct from the proposition "Mary loves John," although the same long-term memory elements may be activated by both. What if one has never met John, does not know which John is being referred to, or has never encountered the name "John" before? The degree to which the content of working memory includes activated long-term memory varies, and semantic and episodic associations activated along with the proposition may vary, but the simple proposition "John loves Mary" can exist in working memory apart from this extra information. As with novel shapes, it may be argued that novel information is retained that does not depend on long-term memories.

The relocation of working memory content from separate buffers, as proposed by Baddeley (1986), to the neural substrates specialized for perception of information is an important and necessary step that will help enable the study of how frontal cortex and attention accomplish that which Ruchkin and his coauthors term "episodic" bindings. Now that neuroimaging methods permit observation of the actual substrates of memory retention, the notion that separate regions exist for buffering and for perception of information could interfere with proper interpretations of neuroimaging results, and is no longer tenable. This is especially true because these buffers were often associated with frontal activity observed during retention, which more likely is involved in attentional control of working memory, as the authors suggest. Long-term memory may become activated as meaningful stimuli, such as words, are retained in working memory, but it is important to remember that humans are facile at retaining novel information, and novel, complex bindings of information. In these instances, the nature of "what is in working memory" transcends the collection of activated perceptual substrates or long-term memories that may be active, especially in the context of research on higher cognition.

Some neuroimaging results suggest that, as the representations bound together in working memory increase in complexity, but not as memory load increases, more anterior regions of prefrontal cortex are recruited (Kroger et al. 2002).

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Abstract: Working-memory retention as activated long-term memory fails to capture orchestrated processing and storage, the hallmark of the concept of working memory. The event-related potential (ERP) data are compatible with working memory as a mental workspace that holds and manipulates information on line, which is distinct from long-term memory, and deals with the products of activated traces from stored knowledge.

Ruchkin et al. equate working-memory retention systems with short-term memory. One advantage of the multiple-component working-memory concept is that it incorporates both on-line processing and temporary memory (e.g., Baddeley & Logie 1999), allowing the concept of working memory as a mental workspace (Logie 1995), rather than as a simple temporary storage device. The notion of working memory retention systems as comprising a state of activated long-term memory fails to capture, or to account for, this concept of orchestrated processing plus storage. A multiple-component working memory, as a mental workspace that is separate from, but holds and manipulates the products of activated traces in long-term memory (Logie 1995; 2003), retains the advantages of offering a testable theory, while accounting for a wide range of behavioural data, both from experimental manipulations and from neuropsychological dissociations (Della Sala & Logie 2002).

Ruchkin et al. argue that it is more parsimonious to assume that short-term memory reflects simply the activation of long-term memory traces, than to assume a separate, multiple-component working-memory system. However, the former theory has to make a wide range of assumptions regarding: the operation of the activation process, how thresholds are set or adjusted, how non-relevant but activated traces are inhibited, how the temporary binding process occurs and is maintained with input from different modalities, how the activated information is manipulated (anything from backward digit recall to generating novel mental images), and how the novel results of those manipulations are held on a temporary basis (for detailed discussion, see Logie 2003). Moreover, a model that explains dual-task interference in terms of similarity of the codes used for each task sounds dangerously circular. Suggesting that two tasks interfere because they use similar codes has some difficulty in making predictions independently of the experimental outcome (Cocchini et al. 2002). In other words, assuming that working-memory retention systems and long-term memory arise from the same conceptual cognitive systems may well be theoretically sterile.

One feature of experimental research into human cognition that is all too rarely recognised is the use of a range of cognitive strategies by participants. Logie et al. (1996) demonstrated that even very simple immediate serial-ordered recall tasks are prone to the use of a range of cognitive strategies, both across individuals, and within the same individual from one occasion to another, even if the aggregate data for the sample of participants generate reliable behavioural phenomena. Indeed, some fMRI data of our own (Logie et al., in press) have shown that specifically instructing participants to use subvocal rehearsal results in a relatively narrow range of areas of activation, focused on Broca's area and the supramarginal gyrus, compared with the much broader network of activation patterns, including those same areas, reported by Paulesu et al. (1993). Interpreting precisely what kind of cognitive function might be employed for any given task requires a very careful cognitive-task analysis, with independent behavioural evidence to indicate precisely how participants are performing the tasks. Without this, at best, the activation patterns can be seen as correlates of how, on average, the participant group performed the task they were set. This is not necessarily informative about the cognitive systems that participants may select to meet the requirements of the task in hand. This kind of detailed cognitive-task analysis is not common in brain imaging studies, and this makes it very difficult to suggest that a given aggregate pattern of activation is reflecting any particular cognitive function. The result may then be a mapping of tasks onto brain structures rather than a mapping of cognitive functions onto brain organisation. In this sense, brain activation patterns might be used to confirm a cognitive theory, but they need not constrain that theory.

The bulk of the evidence described by Ruchkin et al. focuses on the argument that activation of the same brain areas indicates that the same cognitive function is involved. Specifically, because the same brain areas are active for tasks that are assumed to require temporary retention as are involved in activation of stored knowl-

edge or of previous episodes, then there is no need to postulate separate short-term and long-term memory systems. However, different time courses of the task result in different time courses of the ERP trace, a result that could reflect different modes of operation (and hence, functionally different cognitive functions) of the same brain structures. Moreover, maintenance of material on a temporary basis, beyond the end of stimulus presentation, is associated with activity in the prefrontal areas, as well as in the posterior areas, which have been linked to activation of long-term memory. As Ruchkin et al. point out, the advantage of word lists over nonword lists in immediate serial- and free-recall tasks indicates an involvement of semantic information in supporting temporary memory functions. However, there is nothing in the reported ERP data that constrains the interpretation that temporary retention involves areas of the prefrontal cortex, in addition to some form of ongoing activation of the recently activated traces in long-term memory. Temporary memory appears to be associated with both anterior and posterior areas of activation. This could suggest that the prefrontal cortex is the seat of temporary memory, or that both the prefrontal and the posterior activation are required in such tasks, or that the prefrontal activation reflects the operation of some form of controlling mechanism that ensures continued maintenance of long-term memory traces. In all cases, there is a different network of activation associated with temporary memory than with long-term memory tasks, even if there is some overlap in the brain areas involved. At a conceptual level, all three of these interpretations are quite consistent with working memory holding the products of activated traces from long-term memory; they are also consistent with working memory comprising a system that is conceptually quite distinct from long-term memory.

Does sustained ERP activity in posterior lexico-semantic processing areas during short-term memory tasks only reflect activated long-term memory?

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Abstract: We challenge Ruchkin et al.'s claim in reducing short-term memory (STM) to the active part of long-term memory (LTM), by showing that their data cannot rule out the possibility that activation of posterior brain regions could also reflect the contribution of a verbal STM buffer.

Ruchkin et al. argue that they provide strong evidence for a lexico-semantic contribution to verbal short-term memory (STM) tasks, by showing greater event-related potential (ERP) activity in posterior lexico-semantic processing areas (most pronounced in the vicinity of the central midline scalp) during the retention of STM lists of five words compared to STM lists of three nonwords. At an empirical level, we support Ruchkin et al.'s results, as we also observed very similar data in a recent positron emission tomography (PET) study investigating lexicality effects in STM. Collette et al. (2001) explored the activation of posterior brain areas in both a STM task (ordered recall of three words vs. three nonwords) and a control condition (repetition of one word vs. one nonword). When comparing brain regions activated for words versus nonwords in the STM condition, after accounting for brain regions already activated when contrasting words and nonwords in the control condition, we observed greater activation in two posterior brain regions, the left middle temporal gyrus (BA 21) and the left temporo-parietal junction (BA 39). Our data clearly support the idea that posterior brain areas play an active role during short-term retention of words and further complement the data of Ruchkin et al. by providing a more precise localization of these brain regions.

However, at a theoretical level, we consider that there might be an alternative interpretation for the activation of posterior brain regions during STM processing of words than the interpretation put forward by Ruchkin et al. They consider that their data support the position that STM mainly reflects the activated state of LTM, based on similar activation of posterior brain areas thought to encode lexico-semantic language knowledge during both single-word processing and STM for words, relative to single-nonword processing and STM for nonwords. This interpretation includes the implicit assumption that the observed activation of posterior processing areas exclusively reflects the neural substrate of lexico-semantic representations encoded in LTM. However, we think that the results cannot exclude the possibility that the posterior brain areas activated in that study could also reflect the contribution of a STM buffer in addition to activation of lexico-semantic knowledge in LTM. First, the posterior regions encoding lexico-semantic knowledge and those having a buffer function, although different, could be spatially very close and thus difficult to distinguish by ERP techniques, which have a relatively poor spatial resolution. Second, the authors compared recall of five words versus three nonwords in order to achieve a similar level of STM performance for words and nonwords. However, a similar level of performance does not guarantee that the requirements of STM storage capacities are the same in both tasks; it is still possible that STM load was greater in the word than in the nonword condition, especially as the words (five items) had to be maintained longer in STM than the nonwords (three items) before recall. By extension, this implies that the greater ERP activation observed in posterior brain regions during STM for words relative to nonwords could also reflect the activation of a STM buffer, and not only activation of lexico-semantic knowledge as proposed by the authors. Third, we recently showed more directly that posterior brain regions could have a specific STM buffer function for verbal information, by studying brain activation using PET imaging for verbal STM performance in three patients that had recovered from Landau-Kleffner syndrome, a rare epileptic childhood aphasia characterized by persistent verbal STM impairments (Majerus et al. 2003a). The patients were presented lists of four words for immediate serial recall and a control condition (repetition of one word); there was also a control group of 14 healthy young adults. Two of the patients showed reduced activation in left and right posterior superior temporo-parietal areas during the STM condition compared to the control condition, and they presented, at the same time, impaired performance in the STM condition. The third patient showed increased activation in the right posterior superior temporo-parietal area in the STM condition, while presenting, at the same time, relatively normal STM performance. These results suggest that activation of the posterior temporo-parietal area determines very directly the level of performance observed in the STM condition. Furthermore, as there were no differences in behavioural and imaging results between control subjects and the patients for repetition of single words (control condition), which required the same amount of activation of lexico-semantic representations as the STM condition (repetition of word lists), impaired lexico-semantic activation is not likely to account for the results observed in the STM condition. Finally, in a neuropsychological study with the same patients, we explored more directly the relationship between language-processing impairments and verbal STM performance (Majerus et al. 2003b); we showed that all three patients showed no major impairment at the level of lexico-semantic representations, using both standard vocabulary tests as well as more sensitive experimental tasks measuring speed of access to lexico-semantic representations. Furthermore, although two of the patients showed some residual deficits in phonological