

Neural correlates of access to short-term memory

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Behavioral research has led to the view that items in short-term memory can be parsed into two categories: a single item in the focus of attention that is available for immediate cognitive processing and a small set of other items that are in a heightened state of activation but require retrieval for further use. We examined this distinction by using an item-recognition task. The results show that the item in the focus of attention is represented by increased activation in inferior temporal representational cortices relative to other information in short-term memory. Functional connectivity analyses suggest that activation of these inferior temporal regions is maintained via frontal- and posterior-parietal contributions. By contrast, other items in short-term memory demand retrieval mechanisms that are represented by increased activation in the medial temporal lobe and left mid-ventrolateral prefrontal cortex. These results show that there are two distinctly different sorts of access to information in short-term memory, and that access by retrieval operations makes use of neural machinery similar to that used in long-term memory retrieval.

focus of attention | inferior temporal cortex | working memory | medial temporal lobe | functional magnetic resonance imaging (fMRI)

Fundamental questions about the psychological and neural architecture of short-term memory (STM) have been the subject of research for over a century. This interest is fueled by demonstrations that variations in the amount of information that can be held in mind explain differences in IQ, reasoning, reading comprehension, and problem-solving (1–3). Hence, understanding the STM system that affords online maintenance of information will help us understand a great deal about cognition. In this context, two questions have received much attention: “What is the capacity of STM?” and “What is the relationship of STM to long-term memory (LTM)?”

With regard to capacity, converging behavioral and neural evidence has estimated a limit of approximately four items (4–8). A large body of behavioral research has demonstrated sharp performance discontinuities when STM is loaded with more than four items (4). This behavioral evidence is supplemented by neural data showing that areas within the intraparietal sulcus (IPS) and lateral occipital cortex track these patterns of performance, supporting the idea of a capacity limit of four (5–8).

A different line of behavioral research indicates that there are also sharp distinctions between the single most recently processed item in STM and other recently presented items (9, 10). McElree and colleagues examined retrieval times for probes in an item-recognition paradigm (9, 10). The paradigm used rapid presentation and a very short delay interval so that the most recently presented item was presumably in the focus of attention. Retrieval time for the most recently presented item was faster than retrieval times for all other items in the list. Other studies have demonstrated that updating memory representations is substantially more difficult when one must switch the focus of attention between two representations held in mind (11, 12). These results have led to proposals that within memory, a single item lies in the focus of attention and is uniquely immediately accessible for cognitive operations (9–13). Although some authors have interpreted this result to mean that STM is limited to just one item (9, 10), other authors have proposed that the focus of attention is only one of multiple states of items within STM (11, 13). Either way, there does appear to be excellent behavioral evidence to distinguish the

representation of an item within the focus of attention from other items that are not within the focus.

What characteristic distinguishes an item within the focus of attention from other items in STM? One possibility is that compared with other items in STM, the item in the focus of attention is distinguishable from other items simply by greater memory strength. Neurally, this may be realized by enhanced activation in regions of memory storage for the item that is in the focus of attention relative to other items. Such regions of storage most likely include posterior aspects of cortex in the inferior temporal (IT) lobe responsible for recognizing and representing words, objects, faces, and other visual stimuli (14–18). By this account, all items in STM are represented by activation in IT cortex, but an item in the focus of attention may be distinguished by enhanced activation in this region. In fact, several studies have demonstrated maintenance-related activation in IT regions during short-term retention (16–21). However, none of these studies has compared the level of activation of the item presumed to be in the focus of attention with the level of activation of other items. Hence, it remains open whether the focus of attention is represented by enhanced IT activation or whether other neural circuitry is involved.

It is thought that information retained in STM within IT regions is mediated by selection mechanisms of the ventrolateral prefrontal cortex (VLPFC; refs. 13 and 16) and attentional mechanisms of posterior parietal cortex (PPC) (13, 22). The interactions between IT and frontal-parietal attentional regions may be enhanced for the focus of attention relative to other information in STM. Therefore, an item within the focus of attention may also be distinguished by increased synchrony between IT regions of storage on the one hand, and frontal and parietal attentional sites on the other hand. To our knowledge, no research has investigated this matter.

Beyond the focus of attention, what other distinctions can be drawn in memory? Most prominently, researchers have distinguished between information held actively and online in STM and information that is not actively maintained, but is available for retrieval in LTM (23). Much of the evidence in support of this proposal is based on the claim of unique involvement of the medial temporal lobe (MTL) in LTM, but not STM (24, 25). For example, it is often asserted that patients with damage to the MTL demonstrate deficits in LTM, but not STM (24). Moreover, these deficits become larger with increasing time between the study of memoranda and memory tests (26–31). Based on these findings, it has been suggested that the MTL is critical for maintaining associations underlying LTM, but not STM, supporting the idea that STM and LTM represent distinct memory stores (23).

Contradicting classic models of memory, more recent research has demonstrated that damage to the MTL can produce memory deficits with retention intervals as short as 2–10 sec (26–30). Such deficits appear to be especially prevalent when the material to be remembered is novel or involves relational information (30, 32). In

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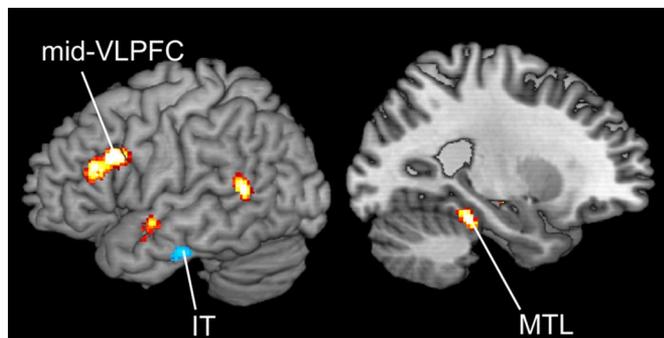


Fig. 2. Left hemisphere rendering of the contrast between the -2 and -3 probes and -1 probes. Contrast maps are thresholded at $P < 0.01$ for display purposes. The -2 and -3 probes $>$ -1 probes in hot colors (increased retrieval demands); -1 probes $>$ -2 and -3 probes in cool colors (focus of attention).

availability for immediate cognitive operation (9–13). As such, an item in the focus of attention does not need to be retrieved *per se*. We speculated from this assumption that regions involved in representing the item in the focus of attention might show heightened activation when a recognition decision was made on that item. This speculation derives from results in the object-based attention literature demonstrating that top-down attentional modulation produces an increase in bottom-up perceptual activation (22, 45). That is, when attentional processes are focused on a representation, a stimulus that matches that representation will produce an enhanced neural response in regions supporting the representation. Similar ideas have been used to explain match enhancement effects in IT cortex, but without explicit mention of a differentiable focus of attention (46, 47). Therefore, although we examined retrieval-related activation here, we argue that this activity should reveal regions supporting the representation of the item in the focus of attention.

Contrasting retrieval-related activation for -1 probes with -2 and -3 probes revealed activation increases in bilateral IT cortex (BA 20/21; Fig. 2; Table S2). The IT regions were somewhat more anterior and lateral to regions previously reported to be involved in short-term maintenance (17–21), a point to which we return in *Discussion*. Post hoc contrasts in these regions revealed that activation for -1 probes differed from all other probe-types [-2 , -3 , and negative, $t(18) > 2.5$, $P < 0.01$ for all tests], but no other probe

types differed from each other [$F(2, 18) = 1.155$ for right IT, $F(2, 18) = 1.047$ for left IT, $P > 0.3$].

To investigate whether activation in the IT regions was related to behavioral performance, we examined correlations between the recency effect (faster responses in RT for -1 probes versus -2 probes), and activation (greater activation for -1 probes versus -2 probes), restricting ourselves to regions showing significant activation differences at $P < 0.01$ (see *SI Methods*). A region of right IT cortex (MNI center: 60, -20 , -18) showed a strong correlation with the recency effect in RT ($r = 0.57$, $P < 0.05$, 15 voxels; Fig. 3A). That is, greater behavioral recency effects were related to greater retrieval-related activation to -1 probes relative to -2 probes. Note that this region did not demonstrate a corresponding primacy effect (i.e., -3 probes $>$ -2 probes, $t(14) < 1$). So, it seems not to be the case that the region simply tracked ease of retrieval; rather, it appears to be associated with facilitation in retrieving the item in the focus of attention.

Functional Interactions with Inferior Temporal Cortex. Having confirmed that right IT cortex was strongly related to behavioral performance, we were interested in investigating whether this region is truly responsible for representing the item in the focus of attention in STM. Current theories of STM posit that the item in the focus of attention is actively maintained via the support of frontal- and parietal-attentional systems (13). That is, ventral regions of the frontal lobe are thought to shield active representations from interference (13–16, 19), and PPC is thought to be involved in maintaining attention on these representations to keep them active (13, 22, 45). To investigate these claims, we performed functional connectivity analysis (44) by using the right IT cortex as a seed. We looked for regions demonstrating greater connectivity with the right IT seed region when responding to -1 probes relative to -2 and -3 probes. This analysis revealed regions that show increased connectivity related to the focus of attention relative to other information in STM.

Confirming our predictions, right VLPFC (Table S3; Fig. 4) demonstrated stronger connectivity with right IT cortex when subjects responded to -1 probes relative to -2 and -3 probes. A similar pattern was also observed in left PPC. This region was lateral to the IPS region that has been demonstrated to correlate strongly with capacity (Fig. S1; refs. 5–8).

MTL and Left Mid-VLPFC Contributions to STM Retrieval. The differences in retrieval times for -1 , -2 , and -3 probes provided a parametric assay of retrieval demands that mirrored previous

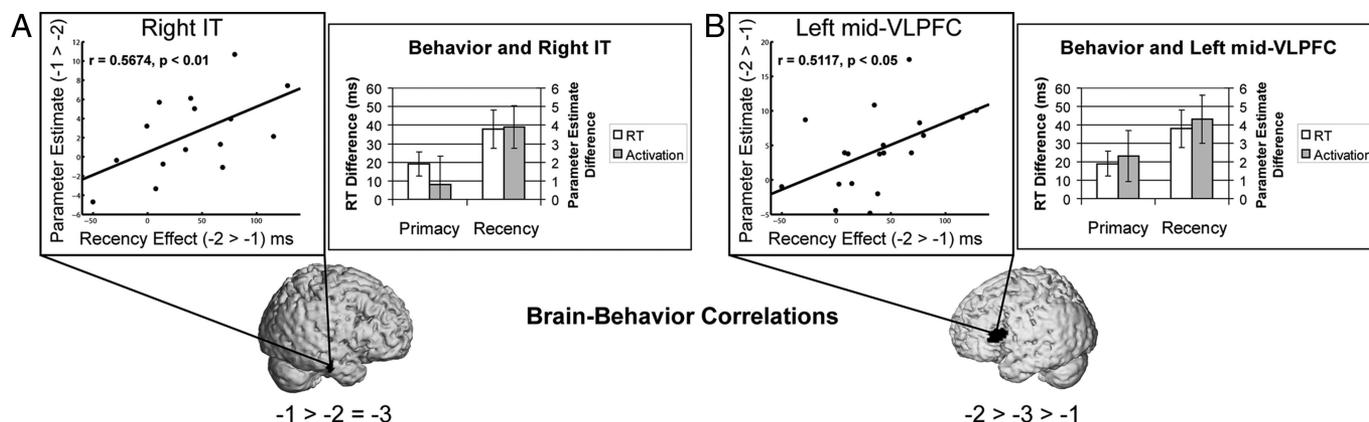


Fig. 3. Brain–behavior correlations. (A) The recency effect in RT, indexed by faster responses for the -1 probes relative to -2 probes, showed a strong correlation with activation increases for the -1 probes relative to -2 probes in right IT cortex (Left). The bar graph (Left) demonstrates that although there was a significant recency effect in brain activation, there was no corresponding primacy effect (-3 probes $>$ -2 probes). Hence, this region appears to be uniquely associated with the focus of attention. (B) The recency effect in RT showed a strong correlation with activation increases for the -2 probes relative to -1 probes in left mid-VLPFC (Right). The bar graph (Right) demonstrates that activation patterns mirrored behavioral recency and primacy effects (slower responses to the -2 probes relative to -3 probes and greater activation for the -2 probes relative to -3 probes). Hence, this region appears to vary with retrieval demands.

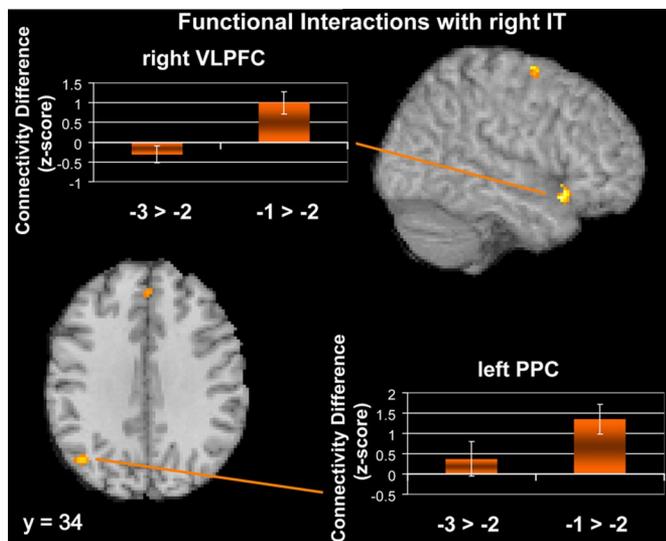


Fig. 4. Regions demonstrating functional connectivity increases with right IT cortex for -1 probes relative to the -2 and -3 probes. Results suggest that the focus of attention is mediated by top-down biasing from the right VLPFC and the left PPC. The bar graphs demonstrate that although these regions show connectivity increases that correspond to recency effects (-1 probes $>$ -2 probes), there were no commensurate primacy effects (-3 probes $>$ -2 probes). Therefore, these regions appear to be associated exclusively with enhanced connectivity related to the focus of attention.

studies (9, 10). Hence, based on the RT data, we hypothesized that retrieval demands were greatest for -2 probes, next greatest for -3 probes, and least for -1 probes. We further hypothesized that -1 probes required minimal use of retrieval processes because this item was presumed to be in the focus of attention and hence available for immediate cognitive operation. Therefore, we used activation to -1 probes as a baseline to index retrieval demands in STM.

Based on the rationale above, we hypothesized that regions involved in STM retrieval would demonstrate heightened activation to -2 and -3 probes relative to -1 probes. If retrieval dynamics in STM mimic those of LTM, we would expect increases in the MTL and left VLPFC as a reflection of retrieval demands. Confirming this hypothesis, compared with -1 probes, -2 and -3 probes produced enhanced retrieval-related activation in left parahippocampal and entorhinal cortex of the MTL [Brodmann's area (BA) 36 and 35]. Activation increases were also observed in left lateral prefrontal cortex, both in mid-VLPFC (BA 45) and more dorsal regions (BA 9 and 46) (Fig. 2; Table S4). The left PFC region was in the opposite hemisphere and 3 cm superior to the region that showed connectivity with the IT cortex, indicating that it is not part of the network involved in representing the item in the focus of attention. Post-hoc contrasts within these regions demonstrated that both MTL and left PFC showed strong recency effects, with greater activation for -2 probes relative -1 probes [$t(18) = 3.65$, $P < 0.001$ for MTL; $t(18) = 4.1$, $P < 0.001$ for left PFC], and marginal primacy effects, with greater activation for -2 probes relative to -3 probes [$t(18) = 1.7$, $P = 0.05$ for MTL; $t(18) = 1.62$, $P = 0.06$ for left PFC]. These activation results reflected the behavioral effects and demonstrated that these regions vary parametrically with retrieval demands.

To bolster the claim that the MTL and left PFC are retrieval-related, we examined whether activation differences in these regions correlated with behavioral performance. Mirroring the analyses above, we searched for regions where the behavioral recency effect measured by the RT difference between -1 probes and -2 probes predicted brain activation differences between -1 and -2 probes. We restricted this analysis to regions that demonstrated

greater activation for -2 probes relative to -1 probes at $P < 0.01$.[†] Left mid-VLPFC (MNI center $-58\ 24\ 20$, BA 45) demonstrated a strong positive correlation with the behavioral recency effect ($r = 0.51$, $P < 0.05$, 33 voxels; Fig. 3B). As demonstrated in Fig. 3B, this region also showed a marginal primacy effect with greater activation for -2 probes relative to -3 probes [$t(18) = 1.69$, $P = 0.054$]. These results closely mirrored the behavioral data and suggest that the left mid-VLPFC responds to increased retrieval demands. Similar results were found in the MTL (see *SI Results*).

Functional Interactions with Left Mid-VLPFC. To understand the mechanisms by which left mid-VLPFC participates in short-term retrieval, we performed functional connectivity analysis, searching for regions demonstrating increased correlation with the left mid-VLPFC for -2 and -3 probes relative to -1 probes (44). That is, we wished to explore what regions covary with the left mid-VLPFC with increased retrieval demands. This analysis penetrates the mechanisms by which retrieval is achieved.

The results revealed that the left mid-VLPFC demonstrated increased connectivity with the hippocampus with increasing retrieval demands (Table S5). Increased functional connectivity was also observed in posterior superior temporal regions near Wernicke's area, occipital cortex, anterior superior temporal gyrus, and ventromedial prefrontal cortex (Fig. 5). These results suggest that as retrieval demands increase, the left VLPFC accrues information from several memory sources to arrive at a correct decision. These sources include phonological information (Wernicke's area; ref. 48), semantic information (anterior superior temporal gyrus; ref. 49), contextual information (hippocampus; refs. 50 and 51), and visual information (occipital cortex).

Discussion

Recent psychological models include the assumption that of the information in STM, a single item resides in the focus of attention that is available for immediate processing without explicit retrieval needing to operate on that item (9–13). The results presented here suggest that the item in the focus of attention in STM is represented by enhanced activation in IT cortex. This region demonstrated a strong correlation with behavioral measures of retrieval facilitation associated with the focus of attention, solidifying the idea that it performed a central role in the task.

Corroborating unitary models of memory (13, 32, 33), we found regions of the MTL and left mid-VLPFC involved during short-term retrieval. These regions varied with retrieval demands and demonstrated strong correlations with behavioral measures of retrieval processes. Furthermore, we demonstrated that the MTL varied with retrieval demands in STM by using both traditional univariate analyses and functional connectivity analyses with an independent seed. The combination of these methods provides robust support for MTL involvement in STM. These results demonstrate that processes of STM retrieval mimic those of LTM, suggesting common mechanisms between STM and LTM.

Role of Inferior Temporal Cortex in the Focus of Attention. Examinations of STM have demonstrated maintenance-related activation in IT regions involved in perceptual representations of objects (17–20) and words (21). Much of this work was inspired by non-human primate studies that demonstrated stimulus-specific delay activity in IT cortex during short-term retention tasks (52, 53). The regions we demonstrated here were somewhat anterior and lateral to regions found in previously published fMRI investigations

[†]We used only the recency effect as a covariate in this analysis to mirror the analyses done on IT cortex and to provide an unbiased way to check to see whether these regions also demonstrated a corresponding primacy effect. However, this analysis could also be done by contrasting -3 and -2 probes with -1 probes by using a $P < 0.005$ activation threshold as in the whole-brain analyses and correlating activation with the same difference in RT. This analysis produced similar results in the left mid-VLPFC ($r = 0.595$, $P < 0.01$) and the MTL ($r = 0.59$, $P < 0.01$).

but spared STM (24). Our connectivity data suggest that multiple sources of information are used in short-term retrieval, including phonological, semantic, and sensory information. These multiple routes to retrieval may overcome the loss of contextual information that accompanies MTL damage. That is, although patients with MTL damage may not be able to place a particular memory item in time, they may still be able to determine that an item is familiar because of a match with a recently activated phonological, semantic, or sensory code. These routes may not be available (i.e., no longer active) for long-term information that was processed in the distant past, producing the previously observed dissociations. Consistent with these ideas, MTL damage produces deficits in short-term retention when the retained information is novel, but not when information is well learned (32). Novel information cannot rely on many of the various representational sources that we found here by using well learned words. Therefore, when alternative routes are not available, the brain may rely exclusively on the MTL for short-term retention (13, 32, 33).

Materials and Methods

Materials and Procedure. Each trial began with a 0.5-s tone followed by a 0.5-s warning fixation cross. Thereafter, the target-set of three words was pre-

sented sequentially, with each word shown for 0.5 s each, followed by a mask for 0.3 s. Finally, a recognition probe was presented for 0.7 s, followed by a 14-s intertrial interval (Fig. 1). Subjects either affirmed the probe as a member of the target-set with a left index press (positive probe) or rejected it as an unrepresented word with a right-index press (negative probe). Half of the probes were not members of the target set and half were members. One-third of the positive probes matched the most recently presented item (−1 probe), one-third matched the item presented before that (−2 probe), and one-third matched the least recently presented item (−3 probe). Words were drawn randomly without replacement from a set of 171 four-letter nouns, and the list was rerandomized after it was exhausted. Subjects performed 6 runs of the task, and each run consisted of 30 trials.

Whole-brain analyses were conducted by using the General Linear Model implemented in SPM2. Probe-locked predictors were convolved with a canonical hemodynamic response function and contrast images for each participant were subjected to a random-effects group analysis.

See *SI Methods* for additional details.

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