

# Memory Retrieval and the Functional Organization of Frontal Cortex

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## Introduction

To be adaptive, the long-term memory system must support retrieval of previously stored knowledge that has high utility given our current task and goals. In this framing, the problem of memory retrieval concerns balancing the recovery of useful information on the one hand against the inherent costs associated with retrieval itself (Anderson and Milson, 1989). Central to striking this balance is cognitive control function (sometimes called executive function), or the ability to leverage abstract goals and contextual representations in order to adaptively influence retrieval and memory-based performance.

The prefrontal cortex (PFC) is necessary for cognitive control function, including during the cognitive control of memory. Whereas damage to medial temporal lobe (MTL) structures produces amnesia that catastrophically impairs the encoding of new information and retrieval of recently encoded information (Scoville and Milner, 1957), damage to the PFC results in more subtle memory deficits (Moscovitch, 1992; Stuss and Alexander, 2005). For example, PFC patients are impaired in contexts that require retrieval of specific information (i.e., source memory tasks; Janowsky *et al.*, 1989; Swick, Senkfor, and Van Petten, 2006), reliance on retrieval strategies (Moscovitch and Melo, 1997), overcoming interference (Moscovitch, 1982; Squire, 1982; Winocur, Kinsbourne, and Moscovitch, 1981), ordering information at retrieval (Shimamura, Janowsky, and Squire, 1990), or retrieval with limited cue support (e.g., free recall; Janowsky, Shimamura, and Squire, 1989; Jetter *et al.*, 1986; Stuss *et al.* 1994). Neuroimaging studies have similarly implicated PFC in relation to specific manipulations of cognitive control at retrieval (Badre and Wagner, 2007; Fletcher and Henson, 2001; Rugg and Wilding, 2000). Thus, PFC is a crucial component of the system that supports cognitive control of memory.

In general, the mechanism of cognitive control can be described in terms of a process of guided activation (Miller and Cohen, 2001), wherein contextual or goal information is maintained in working memory and thereby has the opportunity to provide a top-down influence on processing elsewhere. Nevertheless, a central debate

in the study of cognitive control concerns whether cognitive control is a unitary process or involves a diverse set of functionally distinguishable control processes (e.g., Cooper, 2010).

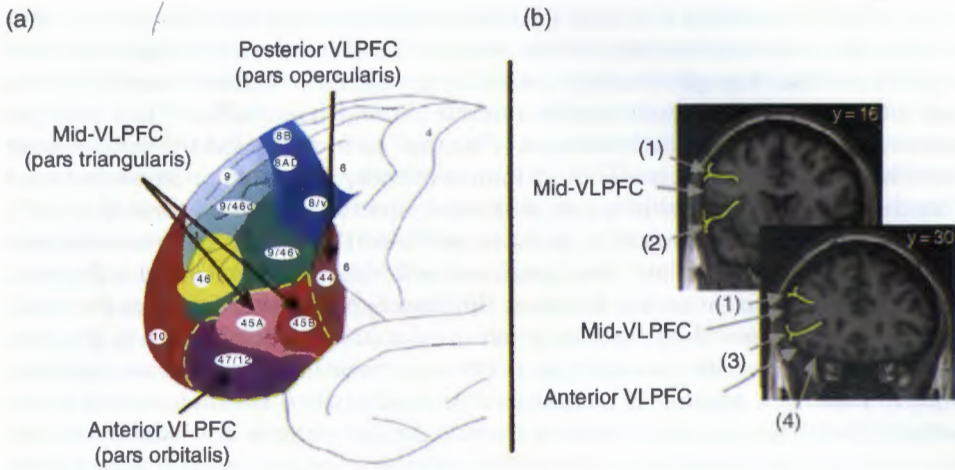
Mirroring the debate about the componentiality of cognitive control, the PFC is likely not a functionally homogeneous structure supporting a unitary executive, but may contain distinct subsystems that support different forms of cognitive control. Neuroimaging studies have provided the primary evidence in favor of functional dissociations in PFC (Badre and Wagner, 2007; Simons and Spiers, 2003; Spaniol *et al.*, 2009). Though debate still exists as to whether there are undifferentiated “multiple-demand zones” within the PFC – such as within the mid-dorsolateral PFC (Duncan, 2010) – it seems now widely accepted that functional distinctions likely exist, such as between ventral and dorsal lateral PFC (Petrides, 2002; Simons and Spiers, 2003), rostral versus caudal PFC (Buckner, 2003; Race, Shanker, and Wagner, 2008), left versus right lateral PFC (Nolde, Johnson, and Raye, 1998; Tulving *et al.*, 1994), and lateral PFC versus medial and subcortical systems (Kuhl *et al.*, 2008; Scimeca and Badre, 2012). Considerable controversy remains, however, regarding the validity of these distinctions and how to map them onto both individual experimental tasks and real-world behavior.

The cognitive control of memory is also likely componential, emerging from a set of interacting component processes. For example, cognitive control has the opportunity to influence retrieval performance in several ways, ranging from processes that structure inputs to the memory system (e.g., cue elaboration) to output control that monitors the outcome of retrieval and selects which representations are permitted to influence decision and action (Benjamin, 2007; see also Chapter 5). These and other distinct memory control processes could likewise be supported by different brain systems. Though research has only begun to refine understanding of these mechanisms and their neural correlates, several distinctions have been proposed regarding differential control processing in the PFC (e.g., Badre and Wagner, 2007; Nyberg, Cabeza, and Tulving, 1996; Simons and Spiers, 2003; Spaniol *et al.*, 2009; Tulving *et al.*, 1994).

Here we will focus on an example of functional specification within PFC related to cognitive control of memory retrieval. We will discuss the hypothetical specialization within ventrolateral PFC (vlPFC) between controlled retrieval and post-retrieval selection/monitoring operations. We will conclude by broadening the discussion of this distinction to consider the participation of these PFC subregions within distinct larger-scale functional networks.

## Venterolateral PFC and the Two-Process Model

The left vlPFC refers to the broad region of lateral frontal cortex that is ventral to the inferior frontal sulcus and rostral to premotor cortex (Figure 7.1). Investigation of the function of this region has long provided the strongest evidence in favor of functional specialization within PFC, from the classic studies of language impairment by Paul Broca (e.g., Broca, 1861) to early functional magnetic resonance imaging (fMRI) studies that distinguished subregions within left vlPFC related to the domain of verbal processing (e.g., the semantic versus phonological distinction; Poldrack



**Figure 7.1** Anatomical divisions of vLPFC. (a) Schematic representation of the cytoarchitectonic divisions of the lateral PFC (adapted from Petrides and Pandya, 2002). Labels highlight the anterior vLPFC (pars orbitalis (~ Brodmann area [BA] 47)) and mid-vLPFC (pars triangularis (~ BA 45)). (b) Coronal slices from the Montreal Neurological Institute (MNI) canonical brain depict the anatomical boundaries that define mid-vLPFC and anterior vLPFC (reprinted with permission from Badre and Wagner, 2007). Labeled anatomical boundaries are (1) inferior frontal sulcus, (2) insular sulcus, (3) horizontal ramus of the lateral fissure, and (4) orbital gyrus.

*et al.*, 1999). More recent work has focused on functional distinctions within this region as they relate to the cognitive control of memory. Specifically, recent work in our lab and in others has focused on a distinction between controlled retrieval, supported by anterior vLPFC, and post-retrieval selection, supported by mid-vLPFC (Badre and Wagner, 2007). Here, we will consider the evidence for and against this potential distinction within left vLPFC.

To illustrate the distinction at the process level between controlled retrieval and selection, it is helpful to consider the analogy of searching for specific information on the Internet. For example, consider that you wish to find information about our lab. First, you need to “hit” our link from the broad, latent associative structure of the web. To do this, you devise a particular keyword to put in your web browser. Of course, some keywords will be more effective than others. For example, searching for “Badre lab” is likely to produce our lab’s website as the top link. However, a less effective search, such as “science lab,” would make it unlikely that you would find the link to our lab without a prohibitive cost in browsing time. Similar to this example, controlled retrieval refers to strategically guiding the activation of task-relevant information from its latent state. In human memory, controlled retrieval can progress by focusing on or elaborating effective cues and thereby increasing the likelihood that task-relevant information is activated from memory. From this perspective, one means of manipulating controlled retrieval experimentally is to reduce the strength of association between salient cues and target knowledge that would support automatic, cue-driven retrieval. In these cases, a top-down influence can aid in activating relevant knowledge from memory.

Importantly, however, it is very difficult to devise even a pair of keywords in a search engine that produce only a single web link. (In fact, it is rare enough that there is a hobby called “Googlehacking”, whereby people try to achieve fame by finding pairs of keywords that produce only one hit through Google™.) Thus, once we retrieve information into our browser, we “browse” or further select the links we want from this limited retrieved set. Though human memory is different in important ways from the Internet, it is a similarly vast, associative structure that uses a form of priority, such as previous co-occurrence, to rank the likelihood that a given representation will be retrieved given a particular cue (Anderson and Milson, 1989; Griffiths, Steyvers, and Firl, 2007). But, as on the Internet, this associative structure ensures that multiple representations will be retrieved given any cue, and that the highest-ranked representation may not be the one that is needed, given current goals and decision criteria. Thus, it is adaptive if a controlled retrieval system is complemented by an output control system that maintains current decision criteria and selects relevant items from among competitors in working memory. The process of selecting from among retrieved information is termed post-retrieval selection. From this perspective, manipulations of response or decision criteria or varying the degree of competition among retrieved representations should affect post-retrieval selection.

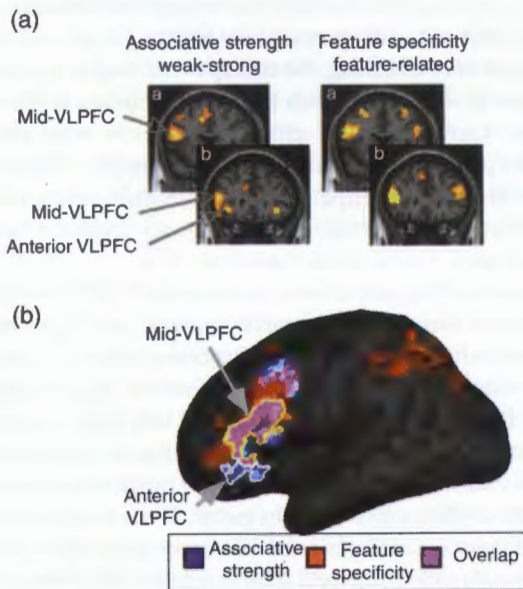
Multiple lines of evidence support the involvement of left vIPFC in the cognitive control of memory. Functional neuroimaging studies, including using fMRI and positron emission tomography (PET), have repeatedly demonstrated greater activation in vIPFC under conditions of effortful or goal-directed retrieval, such as controlling phonological and semantic representations (e.g., Gold *et al.*, 2005), retrieving items with weak versus strong cue support (e.g., Badre *et al.*, 2005), overcoming proactive interference (e.g., Öztekin and Badre, 2011), and active inhibition of memories (e.g., Anderson *et al.*, 2004). Moreover, disruption of vIPFC due to neurological damage or disease decreased patients’ ability to select among competing information (Metzler, 2001; Thompson-Schill *et al.*, 1998). Similarly, intraoperative stimulation (Klein *et al.*, 1997) or application of transcranial magnetic stimulation (Devlin, Matthews, and Rushworth, 2003; Gough, Nobre, and Devlin, 2005) disrupts performance when participants are required to retrieve semantic information. Thus, in broad terms, vIPFC makes a necessary contribution to cognitive control of memory retrieval. However, an ongoing debate concerns the precise nature of vIPFC contributions to memory retrieval, and its functional organization in support of cognitive control.

Drawing on a wide range of declarative memory paradigms, including tests of both semantic and episodic memory, as well as retrieval during action selection, such as task switching, Badre and Wagner (2007) proposed that distinct subdivisions of the rostral left vIPFC support distinct controlled retrieval and post-retrieval selection processes, associated with the inferior frontal gyrus (IFG) pars orbitalis (~ Brodmann area [BA] 47) and pars triangularis (~ BA 45), respectively. These subregions were termed anterior vIPFC and mid-vIPFC, respectively (Figure 7.1). We now briefly summarize the evidence that supports this distinction.

The two-process model proposes that anterior vIPFC is activated when memory must be searched in a goal-directed manner (i.e., controlled retrieval; Badre and Wagner, 2007). Accordingly, when bottom-up cues are insufficient to elicit activation of target knowledge (i.e., automatic retrieval), demands on controlled retrieval processes increase. Control can aid retrieval in these contexts by elaborating cues or generating retrieval plans that structure the input to the retrieval system and so make

it more likely that relevant information will be retrieved. Consistent with this hypothesis, anterior vLPFC is consistently activated during semantic retrieval tasks in which the association between available cues and target knowledge is weak. For example, deciding that “candle” is semantically related to “flame” is easier and requires less controlled retrieval than deciding that “candle” is related to “halo,” because the association between candle and halo is weak relative to the association between candle and flame. Thus, experiments that manipulate associative strength, based either on pre-experimental norms (Badre *et al.*, 2005; Wagner *et al.*, 2001) or on associations learned during the experimental session (Danker, Gunn, and Anderson, 2008), consistently show greater activation in anterior vLPFC under weak relative to strong associative strength conditions (Figure 7.2). In a way similar to high cue–target association strength, anterior vLPFC shows repetition suppression effects accompanying the increased semantic fluency that follows repetition of an item during a semantic memory task, even when the decision/response level effects are not repeated (Race, Shanker, and Wagner, 2008).

According to the two-process model, mid-vLPFC is activated under conditions in which multiple items are retrieved from memory, but only a subset must be selected for further processing (i.e., post-retrieval selection; Badre and Wagner, 2007). As described above, automatic and controlled retrieval processes can result in the recovery of multiple representations. Thus, post-retrieval selection is needed to resolve competition



**Figure 7.2** Results from manipulations of control during semantic retrieval provide evidence for the two-process model (reprinted with permission from Badre *et al.*, 2005). (a) Contrasts of weak relative to strong associative strength (associative strength) ( $p < 0.001$ ) and decisions of item similarity based on features (e.g., color) relative to general semantic relatedness (feature specificity) ( $p < 0.001$ ). (b) Contrasts of associative strength (blue) and feature specificity (red) and their overlap (purple) are rendered on an inflated MNI canonical surface. Anterior vLPFC was sensitive to associative strength, whereas mid-vLPFC was sensitive to both associative strength and feature specificity.

among the multiple retrieved representations, and to permit selected representations to guide decision and action.

Support for mid-vlPFC and post-retrieval selection comes from several sources. First, mid-vlPFC shows greater activation when participants are asked to decide if two items (e.g., “apple” and “blood”) are similar along a particular dimension, such as color, relative to deciding whether they are generally semantically related to one another regardless of dimension (feature specificity effect) (Badre *et al.*, 2005; Thompson-Schill *et al.*, 1997) (Figure 7.2). This difference is thought to arise because making the decision along a particular task-relevant dimension requires focusing attention only on the retrieved details relevant to the decision and ignoring any other properties. Notably, anterior vlPFC does not show a difference between specific and general decision conditions (Badre *et al.*, 2005).

Proactive interference (PI) occurs when a prior learned association automatically elicits retrieval of information that competes with a current retrieval task (Anderson and Neely, 1996; Postman and Underwood, 1973). PI during short-term item recognition has consistently been associated with increased activation in mid-vlPFC (Badre and Wagner, 2005; Postle and Brush, 2004; Postle, Brush, and Nick, 2004). PI during short-term item recognition does not consistently produce activation increases in anterior vlPFC. However, as discussed below, other manipulations of PI have been associated with anterior vlPFC activation (Öztekin and Badre, 2011).

During lexical decision, an unexpected target produces an interference effect above a neutral baseline. This interference effect is thought to be due to competition between information retrieved during preparation for the target and the information that must be retrieved upon encountering the unexpected target. Competition of this type during lexical decision is associated with increased activation in mid-vlPFC. By contrast, anterior vlPFC shows priming effects consistent with the reduced retrieval demands (Gold *et al.*, 2006). Thus, across these examples, it appears that mid-vlPFC is critical under conditions of competition, presumably when there is a demand to select relevant information for further processing. By contrast, anterior vlPFC is not consistently activated under these circumstances.

Importantly, attempts to directly dissociate anterior and mid-vlPFC are complicated by the fact that, akin to our Internet search analogy, any process of retrieval, be it controlled or automatic, holds the potential for competition. Thus, similar to anterior vlPFC, mid-vlPFC often shows increased activation under conditions requiring controlled retrieval (Badre *et al.*, 2005; Wagner *et al.*, 2001). And so, though single dissociations are sometimes observed (e.g., Danker, Gunn, and Anderson, 2008), double dissociations are less common. However, if one pits competition against associative strength, it is possible to dissociate these regions. For example, when the number of retrieval cues is small (low overall retrieval) but associative strength is weak, there will be more demands on controlled retrieval than selection. By contrast, when the number of retrieval cues is large (high overall retrieval) but associative strength is high, this puts greater demands on selection than controlled retrieval. Consistent with this prediction, Badre *et al.* (2005) directly pitted number of available retrieval cues against associative strength and produced activation in anterior vlPFC but not mid-vlPFC. Thus, crossing the number of retrieval cues (i.e., increasing retrieval demands) with associative strength dissociates anterior from mid-vlPFC; and when this is taken together with the feature specificity effect described above, this produces a region-by-effect interaction, dissociating anterior and mid-vlPFC (Badre and Wagner, 2007).

In summary, there is evidence both across and within studies for dissociable functions between anterior vIPFC and mid-vIPFC during cognitive control of memory, and these functions can be characterized as controlled retrieval and post-retrieval selection respectively. Nevertheless, there have been challenges to the two-process model. These have included formal theoretical arguments about whether two processes are required to achieve controlled retrieval and selection functions, as opposed to a single-process model that can support both functions (Danker, Gunn, and Anderson, 2008; Thompson-Schill and Botvinick, 2006). These models make clear that a single process could achieve these two functions. However, it would seem difficult for a single-process model to account for the empirical dissociation between these processes. There has also been some debate about the nature of the relationship between anterior vIPFC and controlled retrieval, and whether the manipulation of associative strength actually reflects the domain of information being retrieved, such as retrieval of abstract semantics (Goldberg *et al.*, 2007). Again, however, a strictly domain-based account appears too difficult to reconcile with the broader data supporting the controlled retrieval hypothesis, such as the observation of activation in anterior vIPFC when retrieving weak, arbitrary paired associations (Danker, Gunn, and Anderson, 2008).

However, recent years have produced a potentially important challenge to the characterization of post-retrieval selection and its hypothesized relationship with competition. First, Öztekin and Badre (2011) manipulated competition using a release-from-PI paradigm in which competition was quantified for each trial using multi-voxel pattern analysis (MVPA; for more discussion of this method, see Chapters 1, 2, and 6). This procedure estimated the degree to which competing information was active during each memory decision, as reflected in the distributed fMRI activation in lateral temporal cortex. Importantly, these MVPA indices are correlated with behavioral PI effects and forgetting in memory. However, activation in anterior vIPFC, rather than mid-vIPFC, varied with PI conditions. Moreover, a mediation analysis showed that activation in anterior vIPFC mediated the relationship between the MVPA indices and behavioral PI. In other words, anterior vIPFC was associated with competition resolution in this task.

Second, Snyder, Banich, and Munakata (2011) used a latent semantic analysis procedure to independently characterize the cue–target association strength and competition of target words during a verb generation task. Latent semantic analysis evaluates large bodies of texts to build a multidimensional semantic space in which every word can be plotted in terms of its meaning and its similarity to other words' meanings. Any word can be coded both in terms of its distance from another word in the space (i.e., association strength) and its neighborhood density (i.e., competition: how many words cluster closely around that word in the space). Behaviorally, these two demands are separable, consistent with the concept of distinct controlled retrieval and selection processes (Snyder *et al.*, 2010). However, regions of interest (ROIs) in both anterior and mid-vIPFC showed additive activation changes to both manipulations. Thus, again, a more formal definition of competition in memory found sensitivity to this manipulation within anterior vIPFC, suggesting that this factor alone cannot account for the previously observed dissociation.

The Öztekin and Badre (2011) and Snyder, Banich, and Munakata (2011) results call into question the concept of competition during memory retrieval as being a clear distinguishing factor between anterior vIPFC and mid-vIPFC. Reconciling these findings with the empirical dissociations observed elsewhere will be important for understanding both the function of vIPFC and the factors that affect cognitive control

of memory. For example, in Snyder, Banich, and Munakata (2011), competition arose from within the distributed, semantic structure of long-term memory itself. By contrast, prior studies of post-retrieval selection that show selective mid-vlPFC activation have directly or indirectly manipulated control over the decision criteria required to make a response based on retrieved information. Indeed, repeating a concept produces repetition suppression in anterior vlPFC, even when the decision that is made about that concept changes (e.g., categorization based on size versus material type; Race, Shanker, and Wagner, 2008). By contrast, repetition suppression in mid-vlPFC requires both repetition of the concept and the decision (Race, Shanker, and Wagner, 2008). Consistent with peri- and post-retrieval processing, these distinct repetition effects are separable in time, as assessed with electroencephalography (EEG) (Race, Badre, and Wagner, 2010). Hence, as opposed to the presence or absence of competition, the critical factor governing the involvement of anterior vlPFC versus mid-vlPFC may be the locus of competition, either in working memory or in long-term memory, and the mechanisms that are deployed to resolve that competition. Future studies will be required to separate competition from decision manipulations in order to further understand the distinctions between anterior and mid-vlPFC during control of memory.

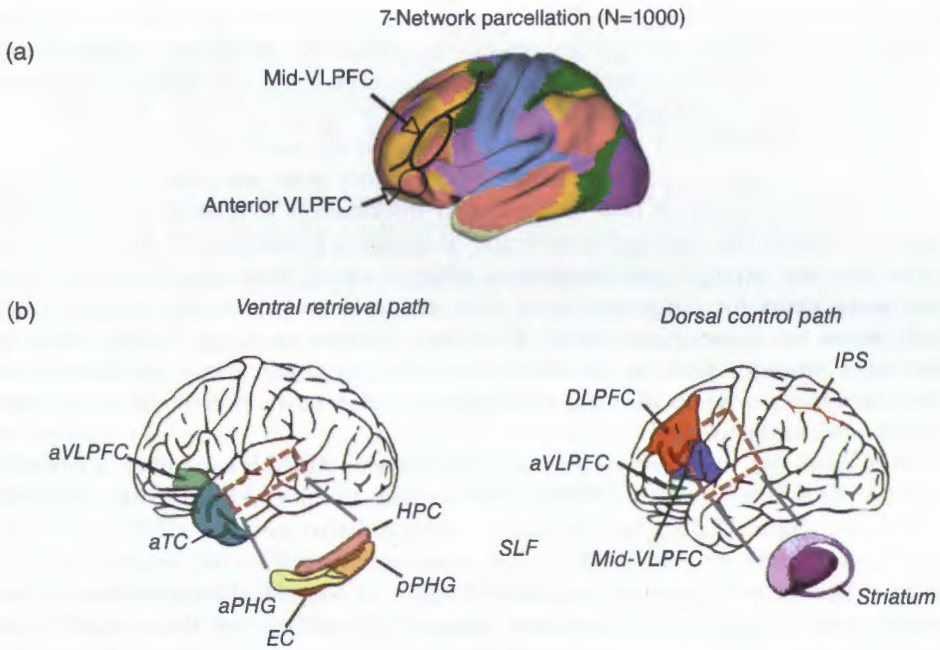
## Separable Functional Frontal Networks

Importantly, subregions of the PFC do not function in isolation. Rather they are participants in larger association networks that dynamically produce controlled behavior. In recent years, functional connectivity analysis of fMRI data (fcMRI) has begun to characterize the networks of regions that may functionally affiliate during particular cognitive or motor tasks or as a consequence of spontaneous activity during rest (Fox and Raichle, 2007; see also Chapter 1). During rest, fcMRI has taken advantage of large samples and datasets in order to parcellate the cortex into different regional groupings that correlate in the low-frequency components of their signal (Buckner, 2010). Among other factors, these low-frequency correlations may reflect the presence of polysynaptic pathways connecting brain regions. Therefore, fcMRI, even at rest, can provide evidence for the presence of functional brain networks. However, given that other factors beyond fixed anatomy likely contribute to these correlations, one should be cautious in assuming that the precise boundaries found at rest will remain fixed across task manipulations. Nevertheless, these networks can provide a helpful guide for generating hypotheses to be tested in task data. Moreover, it may be informative to consider the degree to which the regional distinctions drawn in PFC during control of memory – such as between controlled retrieval and post-retrieval selection – might reflect differences across these broader functional networks.

Of particular relevance to the present discussion, fcMRI across different analysis methods has consistently suggested that roughly ventral versus dorsal frontal regions participate in separable functional networks (Dosenbach *et al.*, 2007; Vincent *et al.*, 2008; Yeo *et al.*, 2011; Figure 7.3A). First, a dorsal frontoparietal network has been repeatedly observed that includes regions of dorsolateral PFC (dlPFC) and posterior parietal cortex, along the intraparietal sulcus. Second, vlPFC and orbital frontal cortex consistently correlate with a network that includes medial and lateral temporal regions,



including hippocampus. This latter network includes many of the regions observed previously in the “default-mode” network (Raichle *et al.*, 2001). However, the division between these two networks is not clearly between the inferior and middle frontal gyrus, which are often labeled vLPFC and dLPFC respectively. Rather, the caudal and dorsal portions of the inferior frontal gyrus cluster with the dorsal frontoparietal control network, whereas the rostral and ventral portions of inferior frontal gyrus cluster separately. And, as can be observed in Figure 7.3a, prior definitions of anterior and mid-vLPFC differentially fall on these separate networks, in that anterior vLPFC consistently falls in the ventral network, whereas mid-vLPFC falls on both or strictly on the dorsal network. This pattern raises the prospect that the observed difference between anterior vLPFC and mid-vLPFC may be reflective of a broader distinction among functional networks (Figure 7.3b).

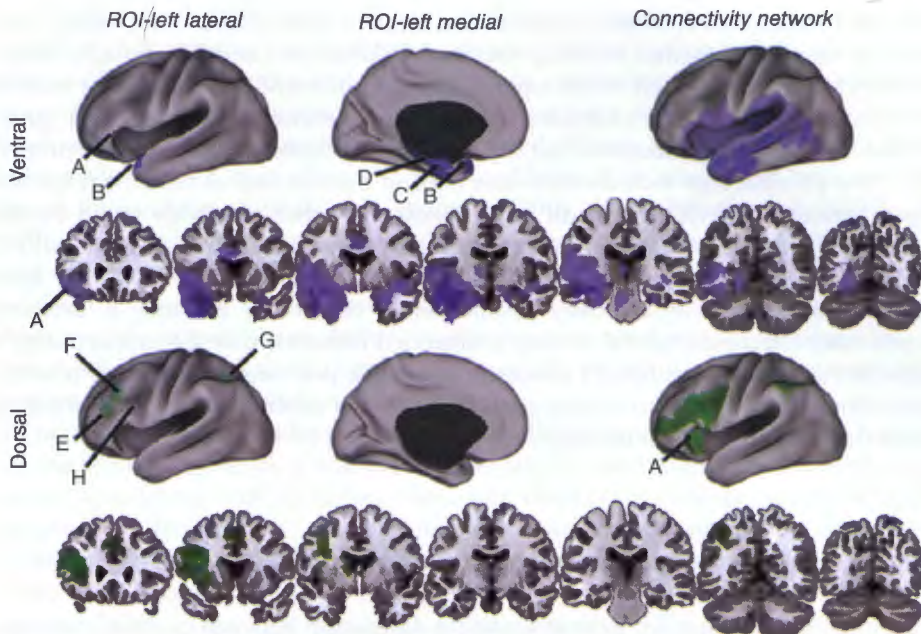


**Figure 7.3** Schematic representation of separable controlled retrieval and post-retrieval control networks. (a) Seven-network cluster in a sample of 1000 participants (reprinted with permission from Yeo *et al.*, 2011) with locations of inferior frontal sulcus (thick line), and anterior and mid-vLPFC regions (circles), indicated. Note that these are approximate locations for illustrative purposes and have not been established formally. Anterior vLPFC falls within the ventral network (red), whereas mid-vLPFC falls on both the dorsal control network (orange) and the ventral network (red) or strictly on the former. (b) Proposed distinction between the ventral controlled retrieval network and the dorsal frontoparietal post-retrieval control network. The ventral controlled retrieval network includes anterior vLPFC (aVLPFC), anterior temporal cortex (aTC), anterior parahippocampal gyrus (aPHG), and hippocampus (HPC), whereas the dorsal frontoparietal post-retrieval control network includes dorsolateral PFC (DLPFC), and inferior parietal lobes (IPS). Other abbreviations: EC, entorhinal cortex; pPHG, posterior parahippocampal gyrus.

Our lab recently tested this hypothesis by analyzing functional connectivity during an episodic memory retrieval task (Barredo, Öztekin, and Badre, 2013). Participants performed a single-agenda source monitoring or exclusion task (Jacoby, 1991). Specifically, at encoding participants performed one of two semantic decisions with words (size or organic). Then, at test, they verified whether they had performed a target source task with each word, indicating yes or no. Importantly, we assume that any evidence of an item being old drives a tendency to endorse the item. Thus, these “incongruent” items, in which the correct response for the source decision is “no” despite the studied items themselves being familiar to the subject, produce decision or response-level conflict in order to either reject the evidence of oldness as not diagnostic for the source decision and/or to override the positive response. This conflict is evident in increased reaction time (RT) and errors for these incongruent items relative to congruent items (which were seen with the target source task and entail a “yes” response). Beyond congruency, we also manipulated the association strength between item cues and target source information by varying repetition during encoding. A single encounter with an item at encoding should produce a weaker memory trace associating that item with its source task compared to multiple repetitions. So greater controlled retrieval should be required on weak associative strength trials.

Importantly, controlled retrieval is only affected by associative strength, and is insensitive to congruency. This is because congruency does not affect the likelihood of retrieval, but concerns how remembered information is related to the current response criteria. By contrast, post-retrieval decision processes will show an interaction between strength and congruency, wherein strong items are easier to endorse than weak items for congruent trials, but strong items are harder to reject than weak items for incongruent trials. Therefore, regions showing a main effect of associative strength without an interaction with congruency may be sensitive to retrieval, whereas regions showing a strength-by-congruency interaction are sensitive to post-retrieval factors.

Using this logic, we observed evidence that anterior vIPFC is a member of a ventral retrieval pathway whereas mid-vIPFC affiliates with the dorsal frontoparietal control system (see Figure 7.3b). Specifically, we observed that anterior vIPFC and other regions along the ventral pathway, such as anterior temporal cortex, anterior parahippocampal gyrus, and hippocampus, showed effects of controlled retrieval that did not interact with congruency. Functional connectivity analysis of these functionally defined seeds confirmed that they were members of a common correlated network, specifically correlating more with one another than with regions outside of the network. By contrast, mid-vIPFC showed an interaction between strength and congruency in the univariate analysis and was functionally connected to dlPFC and inferior parietal regions that are members of the frontoparietal post-retrieval control network (Dosenbach *et al.*, 2007; Vincent *et al.*, 2008; Yeo *et al.*, 2011). Mid-vIPFC did not correlate with the ventral retrieval network. Notably, in addition to coupling with the ventral retrieval pathway, anterior vIPFC also correlated with mid-vIPFC and the dorsal frontoparietal post-retrieval control network (Figure 7.4). This finding potentially suggests that anterior vIPFC acts as a hub, coordinating processing between the ventral controlled retrieval system and the dorsal post-retrieval control system. But the precise functional significance of this observation is an important question for future work.



**Figure 7.4** Functional connectivity along the ventral controlled retrieval network and the dorsal frontoparietal post-retrieval control network (reprinted with permission from Barredo, Oztekin, and Badre, 2013). Anterior vlPFC functionally couples with aTC, aPHG, and HPC (purple, top). Mid-vlPFC functionally couples with dlPFC, IPS, inferior temporal gyrus (ITG), and basal ganglia (green, bottom). Comparison across networks illustrates that the overlap between frontoparietal control network and retrieval network is primarily limited to aVLPFC. All contrasts are valid  $\{AND\}$  conjunctions from false discovery rate (FDR)-corrected seed maps thresholded at  $p < 0.05$ . Some of the major structures functionally coupling with various seeds are labeled as follows: (A) aVLPFC, (B) aTC, (C) aPHG, (D) HPC, (E) lateral PFC (PFC<sub>l</sub>), (F) lateral posterior PFC (PFC<sub>lp</sub>), (G) IPS, and (H) mid-vlPFC. Note that mid-vlPFC lies within the sulcus and cannot be seen in lateral view; approximate location only is marked.

These results provide a broader context for the previous distinctions between anterior vlPFC and mid-vlPFC. Specifically, prior work has defined vlPFC synonymously with the inferior frontal gyrus and has drawn distinctions – such as between anterior vlPFC and mid-vlPFC – within this anatomically defined region. However, as noted above, the functional boundary between these networks may not be at the inferior frontal sulcus. Rather the dorsal frontoparietal post-retrieval control system includes the middle frontal gyrus and the caudal and dorsal portion of the inferior frontal gyrus. Thus, purely as a matter of location within the inferior frontal gyrus, prior definitions of anterior vlPFC are more likely to fall on the ventral controlled retrieval network, and definitions of mid-vlPFC are more likely to fall on the frontoparietal post-retrieval control network or to be on the border of both retrieval and post-retrieval control networks.

In this regard, it is notable that tasks previously observed to activate dlPFC are those that manipulate post-retrieval monitoring (Rugg, Otten, and Henson, 2002; Rugg and Wilding, 2000), active inhibition of memories (Anderson *et al.*, 2004;

Butler and James, 2010; Depue, Curran, and Banich, 2007; Kuhl *et al.*, 2008), and relational operations within working memory (Blumenfeld and Ranganath, 2007; Fletcher *et al.*, 1998). Based on the operational definitions of these functions used in the literature, it is difficult to draw a clear process distinction between these post-retrieval/decision-level functions and the concept of post-retrieval selection outlined above. It is possible that such distinctions exist and there is further functional specialization between mid-vlPFC and dlPFC. However, another possibility raised by the connectivity analysis is that this process similarity reflects the fact that mid-vlPFC should be functionally grouped with this broader dorsal network. Hence, at least one key functional neuroanatomic distinction in control of memory is between (1) processes affecting retrieval directly (controlled retrieval) that are supported by a ventral retrieval network and (2) processes operating post-retrieval to align remembered information with current task goals and decision criteria that are supported by a more dorsal frontoparietal network.

### Transient Dynamics within Frontal Networks

In the previous sections, we have described a distinction between control processes that operate to influence retrieval itself versus those that operate post-retrieval to align retrieval with task goals and decision criteria. Evidence from fMRI has suggested that this distinction is supported by distinct neuroanatomical subsystems. The temporal resolution afforded by EEG has provided complementary evidence for this distinction (for more on EEG, see Chapter 16). First, these peri- and post-retrieval processes should be distinguishable temporally. Event-related potential (ERP) studies have shown early posterior (~400 ms post-stimulus onset) and late right frontal (~1000 ms post-stimulus onset) differences between correctly recognized old and new items (“old/new effects”) during source retrieval (Allan, Wilding, and Rugg, 1998; Wilding and Rugg, 1996), supporting the presence of multiple temporal components during retrieval. Race, Badre, and Wagner (2010) more directly related early and late ERP components to retrieval and post-retrieval decision and response processes. Participants were asked to make semantic decisions about presented items. Items were repeated during the experiment, sometimes with the same decision and sometimes with a different decision, allowing item-semantic priming to be separated from decision-related priming effects. In ERP, the item priming occurred at an earlier stage than the decision priming, consistent with modulation of early retrieval processes versus late decision processes. Thus, the ERP data are largely consistent with two temporally distinguishable components related to retrieval versus post-retrieval decision or monitoring demands. However, given recent insights regarding the importance of at least two broad functional networks to controlled retrieval and selection, data from EEG can also address the nature of neural dynamics within the networks described above.

Although functional connectivity indicates anatomical connections between frontal and posterior brain regions, the mechanism by which these brain regions dynamically interact during declarative memory retrieval has not been specified. It has been proposed that neural oscillations provide the means by which brain areas interact to perform cognitive tasks (Başar and Schürmann, 2001; Miller and Wilson, 2008; Varela

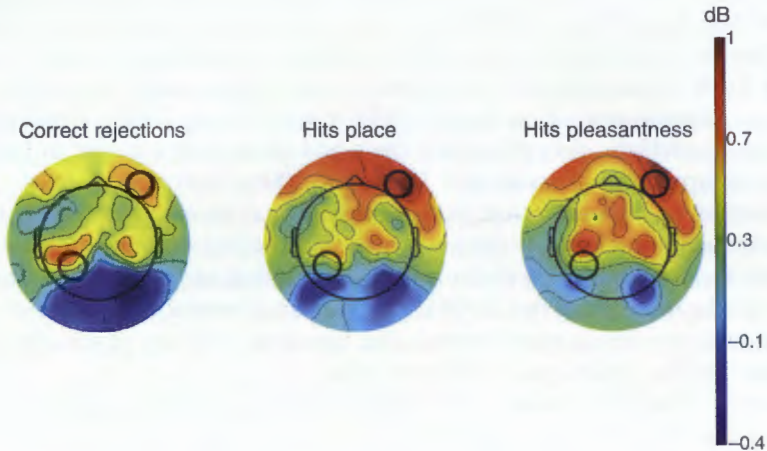
*et al.*, 2001; see also Chapter 2). Fluctuations in postsynaptic potentials produce local oscillations. In addition, oscillators in one brain region can phase synchronize with oscillators in another region through long-range connections. A mechanism for interaction for both local populations of neurons and large neural assemblies is through phase synchronization of oscillations (Miller and Wilson, 2008; Varela *et al.*, 2001). As neurons oscillate, they effectively open and close their window to both send and receive information (Buzsáki and Draguhn, 2004; Womelsdorf *et al.*, 2007). For information to be transferred from one neuronal group to another, the sending neuron must be excitable at the same time that the receiving group is excitable. This requires the coupling of oscillations between sending and receiving neurons through phase synchronization (Fries, 2005). This pattern of neural interaction allows for efficient neural communication through the transient coupling of synchronously firing neurons forming functional neural networks.

There is convincing evidence that neural rhythms contribute to memory retrieval. During episodic retrieval, a number of EEG studies have found greater theta power for hits than for correct rejections. Moreover, differences in theta power distinguish individual differences in episodic memory retrieval performance (reviewed in Nyhus and Curran, 2010). We recently proposed that theta oscillations represent interactions between brain systems for the control of episodic retrieval (Nyhus and Curran, 2010). This hypothesis was initially motivated by studies attempting to localize the sources of theta oscillations during episodic retrieval. In general, theta power increases are frequently observed in frontal scalp locations during successful episodic retrieval, and in frontal and posterior scalp locations for retrieval of specific details of the study episode.

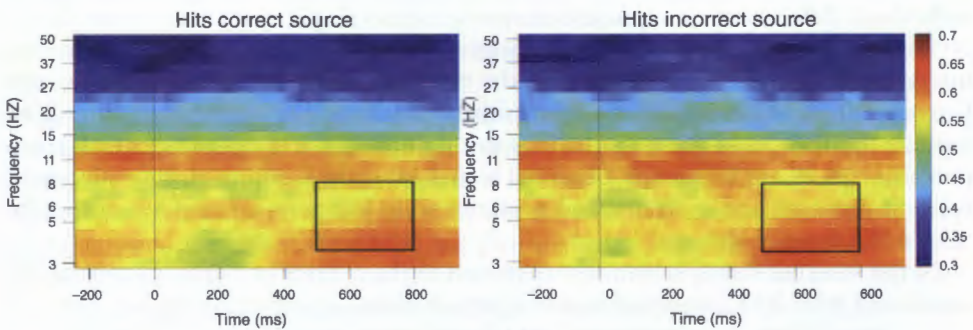
To test whether theta oscillations are related to the control of memory retrieval, we conducted three EEG experiments during which subjects performed a source retrieval task (Nyhus, 2010). Results showed right frontal theta power that was greater for old than new words. In addition, theta coherence between right frontal and left parietal channels was greater for old than new words, for incorrect than correct memory judgments, and for low-confidence than high-confidence response (Figure 7.5). Post-retrieval monitoring demands should be greater when decisions are uncertain, which is more likely for incorrect than correct memory judgments and for low- than high-confidence responses. Therefore, these results suggest that transient theta interactions in a frontoparietal network are involved in the monitoring of episodic memory.

Although these results suggest that theta oscillations are important for communication among brain regions in a post-retrieval control network, future research is needed to localize the source of these effects, and to determine the frequency of communication among the controlled retrieval and post-retrieval control networks. For example, though there are no data on the oscillatory correlates of controlled retrieval as distinct from selection, it is notable that semantic retrieval, which is particularly dependent on anterior vIPFC, has been associated with alpha rather than theta band oscillations. Due to their spatial and temporal limitations, EEG and fMRI methods alone are not sufficient to identify the relationship between oscillations and specific functional networks involved in memory retrieval. Future research simultaneously recording EEG and fMRI is necessary to examine the relationship between oscillatory effects and the functional networks identified with fMRI in declarative memory retrieval.

(a)



(b)



**Figure 7.5** Theta effects during a source retrieval task (reprinted with permission from Nyhus, 2010). (a) Theta power across all channels from 500 to 800 ms. Black circles mark the approximate locations of analyzed channels in right frontal (channel 1) and left parietal (channel 53) brain regions. Color scale: decibel change from pre-stimulus baseline. (b) Theta coherence for all frequencies across one right frontal channel (channel 1) and one left parietal channel (channel 53). Highlighted is theta coherence from 500 to 800 ms. Color scale: magnitude of cross-coherence from 0 to 1, with 0 indicating absence of synchronization and 1 indicating perfect synchronization for each frequency at each time-point.

## Conclusion

In order to deal effectively with our environment, declarative memory systems have developed to adaptively retrieve information that is relevant while outweighing the costs of retrieval. Although information can be automatically retrieved, cognitive control of declarative memory retrieval is important for adaptive retrieval. Here, we have highlighted one functional distinction in the cognitive control of memory that appears to receive support from multiple methods: controlled retrieval versus post-retrieval selection.

As described above, evidence suggests that a ventral retrieval pathway that includes the anterior vLPFC biases memory retrieval when memories are not readily accessible. A more dorsal network that includes mid-vLPFC and potentially dLPFC aligns what

has been retrieved with task goals by selecting appropriate representations, setting decision criteria, and monitoring the outcome of retrieval. These associated networks likely coordinate their activity via oscillations, such as in the theta band for post-retrieval control, the dynamics of which are largely unknown.

Though progress has been made in understanding how the brain controls memory retrieval, a number of fundamental questions remain to be addressed. For example, how are memory control strategies learned, evaluated, and adjusted? What are the neural mechanisms by which PFC can increase the likelihood of retrieval or select relevant items from working memory? How does anterior vIPFC “know” that memory strength is weak and so it is necessary to guide retrieval? Of course, satisfying answers to these questions must be provided without recourse to a “homunculus” or little man in the head who just performs these functions. Rather, formal theoretical and computational models that can incorporate findings from neuroscience data are required. Thus, in our view, considerable progress on these questions will be made by extending existing models of cognitive control to the domain of memory.

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