CHAPTER 9

The Prefrontal Cortex and Human Memory

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The association of damage to the medial temporal lobes (MTL) and hippocampus with impaired memory is one of the classic findings in neuroscience, and the contemporary literature on the cognitive neuroscience of memory is still largely centered on the MTL as the hub of the brain's episodic memory system. Yet the role of the prefrontal cortex (PFC) in memory was recognized as early as the 1930s. Jacobsen (1936), in his classic studies of the delayed-response test in monkeys with frontal lobe lesions, noted that the animals were impaired only when “the differential cues must be supplied by the subject from its past experience” (p. 57). Research on PFC function in the modern era focused on short-term (working) memory until the 1980s, when Milner, Petrides, and their colleagues investigated the effects of focal PFC lesions on tests of long-term contextual memory (Milner & Petrides, 1984). The probing of task-related brain activation with positron emission tomography (PET) in the early 1990s revealed robust PFC activation in association with episodic memory (see Fletcher & Henson, 2001), prompting a surge of neuroimaging and neuropsychological studies on the contributions of the PFC to episodic memory tasks.

These trends can be visualized in Figure 9.1. As evident in the top panel, studies on MTL/

hippocampal function and memory have been published at approximately twice the rate of studies on frontal or PFC function and memory. The lower panel shows a steep increase in studies on the PFC through the 1990s, tapering off in the 2000s. Yet recent developments in functional neuroimaging and analytical tools—in combination with neuropsychological and animal research—continue to yield important new insights about frontal lobe contributions to memory.

The PFC flexibly and dynamically implements domain-general, top-down cognitive control processes, coordinating distributed brain activity in the service of online goals (Miller & Cohen, 2001). These computations support an adaptive function of memory in guiding action in the present and future, as opposed to simply reinstating representations of past experiences. The PFC mediates mnemonic processes related to maintaining, retrieving, manipulating, attending to, biasing, and otherwise coordinating information encoded in the MTL and more modality-specific posterior cortical regions. Functionally specific PFC subregions can be defined by their distinct connections with the MTL and other brain areas, with differential recruitment of these regions according to the task demands and the processing components engaged (Badre

FIGURE 9.1. Trends in publications on the frontal lobes (FL) versus the medial temporal lobes (MTL) and memory. (A) Number of studies on memory and the MTL versus the frontal lobes every half-decade. (B) Increase in studies on memory and the MTL versus the frontal lobes (i.e., difference between each half-decade and the previous half-decade, divided by the previous half-decade). PubMed search terms: “medial temporal lobes OR hippocampus AND memory,” “frontal lobes OR prefrontal cortex AND memory.”

& D'Esposito, 2009; Cabeza & Moscovitch, 2013; Fletcher & Henson, 2001).

In this chapter, we summarize the literature on the role of the PFC in memory tasks. For other, more targeted reviews, see Fletcher and Henson (2001), Simons and Spiers (2003), Szczepanski and Knight (2014), and Nyhus and Badre (2015). Here, we focus our summary of the literature on work not already covered in depth in these reviews; we also cast a wider net, integrating findings from human and animal research across frontal subregions and experimental paradigms. The task is challenging, given the breadth of memory-related processes attributed to the PFC. The psychological and neural architecture of memory has been fractionated into distinct processes and systems (e.g., short-term vs. long-term, encoding vs. retrieval, episodic vs. semantic memory). However, there is evidence that supposedly system- and process-specific neural activity transcends categorical distinctions in the memory literature, as demonstrated by neuroimaging (Ranganath, Johnson, & D'Esposito, 2003) and human and animal lesion studies (reviewed in Fuster, 1995). Furthermore, there are inconsistencies across studies in the division of the PFC. While strict assignment of discrete functions to PFC subregions is questionable (see Duncan, 2001; Wilson, Gaffan, Browning, & Baxter, 2010), some models of the functional organization of the frontal lobes both within memory (e.g., Fletcher & Henson, 2001) and in cognition more broadly (Badre & D'Esposito, 2009) have proven successful in generating new questions and holding up to new evidence.

When possible, we highlight commonalities across tasks and paradigms, adopting a component processing framework (Cabeza & Moscovitch, 2013); yet our review also reflects the literature as it stands, much of which operates from a memory systems framework. We also emphasize recent memory-related research on PFC–MTL interactions and the participation of the PFC in large-scale functional networks, highlighting distributed oscillatory interactions as a mechanism of dynamic network coordination in the service of memory function. We begin by discussing overall functional contributions of the PFC to working, episodic and autobiographical memory tasks. We then discuss distinct PFC subregions and processes that they implement across these measures of memory.

Working Memory

“Working memory” (WM) refers to the temporary and controlled activation and manipulation of mnemonic representations in the service of guiding behavior. It emerges from the coordinated recruitment of a constellation of interacting subprocesses mediated by the PFC (e.g., executive functioning, attention, online maintenance, manipulation) that share the common element of context- and goal-driven modulation of brain activity (Duncan, 2001; Miller & Cohen, 2001).

Most research on the involvement of the PFC in WM has focused on the dorsolateral PFC (dlPFC) (Fuster & Alexander, 1971; Funahashi, Bruce, & Goldman-Rakic, 1989). Following Fuster and Alexander's (1971) discovery of “memory cells” in the lateral PFC whose firing rates tracked mnemonic retention across delays, Goldman-Rakic and colleagues focused on the representational nature of these signals (Funahashi et al., 1989); they argued that higher-order cognition depends on a transition from stimulus-guided to representation-guided behavior, the latter allowing for more complex and adaptive operations (Goldman-Rakic, 1987). According to Baddeley and Hitch's (1974) model, WM is composed of independent, domain-specific, and capacity-limited memory stores (originally the articulatory/phonological loop and the visuospatial sketchpad) and a central executive that coordinates and allocates attention to these “slave” systems. This “standard model” (Postle, 2006) of WM focused on domain-specific temporary storage modules located in the PFC that receive projections from corresponding perceptual regions. In this view, the change in dlPFC cells' firing rate in association with a presented cue, and the sustained firing during delay, reflect transient storage of domain-specific stimulus representations (e.g., Wilson, Scalaidhe, & Goldman-Rakic, 1993).

Yet the standard view requires ever more topographically distinct memory modules or buffers to duplicate the highly modular functional organization observed in more posterior perceptual cortical regions (Postle, 2006). Conversely, single lateral PFC neurons in monkeys have been found to code multiple stimulus properties in memory (e.g., Rao, Rainer, & Miller, 1997; Stokes et al., 2013), and focal lesions in the dlPFC—previously thought to represent space—produce both

spatial and nonspatial WM deficits (Petrides, 1995). Generally, neurons that exhibit feature-selective delay period spiking in a given experiment are often topographically distributed or closely intermingled with cells responding to different types of information (Rao et al., 1997; Duncan, 2001). Spatial WM deficits are observed in human patients only when lesions encompass the whole lateral extent of the PFC, and not the dlPFC selectively (Müller, Machado, & Knight, 2002). These findings suggest that the functional contributions of the PFC to WM are likely to be executive rather than strictly mnemonic, and that these executive computations are distributed rather than localized.

Converging evidence suggests that the PFC is not necessary for the simple storage, rehearsal, or maintenance of information (even though these processes may elicit PFC activity), whereas damage to modality-specific regions produces corresponding impairments in simple maintenance (for a review, see D'Esposito, Cooney, Gazzaley, Gibbs, & Postle, 2006). Models of PFC function suggest that it implements domain-general executive processes by virtue of flexible reciprocal connectivity with posterior cortical representations (Fuster, 1997; Duncan, 2001; Miller & Cohen, 2001). Oscillatory coherence in different frequency bands facilitates the formation of transient networks in WM, allowing for interregional communication (Fries, 2005), and the phase of prefrontal oscillations temporally organizes information held in WM (Siegel, Warden, & Miller, 2009). WM therefore emerges from distributed networks, with the frontal lobes playing a critical role in modulating and coordinating network activity (Fuster & Bressler, 2012; Voytek et al., 2015).

Recent neuroimaging and neuropsychological work challenges the distinction between short- and long-term memory systems (Ranganath & Blumenfeld, 2005; Rose, Olsen, Craik, & Rosenbaum, 2012), suggesting instead a process-specific functional organization of memory in the PFC (Fletcher & Henson, 2001; Ranganath et al., 2003) and the hippocampus (Cashdollar, Duncan, & Duzel, 2011) that cuts across methodological distinctions. In this view, WM and long-term memory (LTM) tasks rely on different brain regions and connections insofar as different control processes are required. Another alternative to the systems-based model is the

view that WM and LTM tasks tap into different activation states in overlapping neural regions, with WM relying on “activity-based” mechanisms emerging out of transient interactions between brain regions, and LTM relying on “weight-based” mechanisms manifested as long-lasting structural changes to synaptic weights formed during encoding and consolidation (Larocque, Lewis-Peacock, & Postle, 2014). These mechanisms are inherently codependent: WM and short-term memory content may be encoded and retrieved minutes or years later, and we may reactivate latent LTM content in goal-directed ways, thereby implicating WM (Atkinson & Shiffrin, 1968).

Episodic Memory

Just as the PFC is not required for simple short-term storage of mnemonic representations, it does not implement episodic memory (EM) encoding or retrieval per se. Rather, the PFC is engaged in higher-order cognitive control processes that modulate the nature and efficacy of encoding, consolidation, and retrieval with respect to current goals and contexts. Thus patients with PFC damage show impairments on tests that require active search, control, manipulation, or monitoring, and on contextual retrieval tasks such as free recall, source recall, or temporal ordering (Davidson, Troyer, & Moscovitch, 2006; Duarte, Ranganath, & Knight, 2005; Wheeler, Stuss, & Tulving, 1995).

Although early research found that PFC damage spares recognition memory for individual items (Janowski, Shimamura, & Squire, 1989), different patterns of PFC damage produce reliable, though sometimes subtle, deficits in recognition memory when there is an executive or episodic (involving reinstating some aspect of the encoding episode) element involved (Stuss et al., 1994; Wheeler et al., 1995). Recognition memory can be accomplished via episodic recollection, which involves retrieving specific contextual details, or familiarity in the absence of specific details (Yonelinas, 2002). Studies using the self-report “remember/know” procedure (in which “remember” responses correspond to recollection; Gardiner, 1988; Tulving, 1985) in patients with lateral prefrontal lesions have yielded mixed results (Duarte et al., 2005; Stamenova et al., 2017; Wheeler &

Stuss, 2003), perhaps because of task differences or patients' difficulty with the metacognitive evaluation required to make the remember/know distinction (Davidson et al., 2006). Lesion location is also a factor, with the lateral PFC critical for retrieving and actively monitoring mnemonic content, and more rostral regions critical for the subjective aspect of recollection (Wheeler & Stuss, 2003; Spaniol et al., 2009). Neuroimaging studies of EM have further identified functional dissociations (for reviews, see Badre & Wagner, 2007; Simons & Spiers, 2003; Spaniol et al., 2009), with the topology of peak activity reflecting the nature of the control process engaged (see below).

Autobiographical Memory

In recent years, there has been a substantial increase in research on autobiographical memory (AM) as a more ecologically valid manifestation of EM. AM is of particular interest to students of PFC function, given the complex and temporally extended nature of AM retrieval and the demand for coordinating multiple component processes. In some cases, results from neuroimaging studies of AM are dissociated from those using laboratory-based assessment of EM (Gilboa, 2004; McDermott, Szpunar, & Christ, 2009), indicating potentially different neural processes contributing to laboratory versus naturalistic memory performance.

Generative strategies necessary for AM retrieval are mediated by executive control operations associated with the PFC, including initiating, guiding, and organizing a memory search, as well as monitoring its recovered content (Kopelman, Stanhope, & Kingsley, 1999). Strategic retrieval deficits in AM have also been studied in depth in relation to psychiatric conditions (Riutort, Cuervo, Danion, Peretti, & Salame, 2003; McKinnon et al., 2015), especially depression, where overgeneral autobiographical retrieval is dominated by categorical and semantic information (Dalgleish et al., 2007); however, MTL damage cannot be ruled out as contributing to this effect, as reduced AM specificity in depression is observed even when strategic retrieval demands are controlled (Söderlund et al., 2014).

AM can be dissociated into an episodic component, entailing the conscious recollection of spatiotemporally specific events from

one's past, and a semantic component, entailing context-independent, fact-like knowledge about the world and oneself (Tulving, 1972; Levine et al., 2004). The phenomenology of episodic autobiographical remembering is characterized by "autonoetic consciousness," the experience of the self as continuous across time. Early research linked autonoetic consciousness to the PFC (Wheeler, Stuss, & Tulving, 1997), and it is of particular relevance, given that conditions associated with PFC dysfunction often produce altered self-awareness (Conway & Pleydell-Pearce, 2000; Kurczek et al., 2015). The quantification of episodic (internal) and nonepisodic (external, usually semantic) details from transcribed AM narratives (Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002) has been fruitful in illustrating the effects of PFC damage (Levine et al., 2004), frontotemporal lobar degeneration (Irish et al., 2011; McKinnon et al., 2008), and aging (Levine et al., 2002) on AM, whereby episodic details are reduced and nonepisodic details are elevated. Similar findings have been reported in relation to imagining future autobiographical episodes (Addis, Wong, & Schacter, 2007), suggesting that the altered processing of AM extends to beyond strictly mnemonic tasks.

In functional neuroimaging studies, AM is associated with distributed and often left-lateralized activity centered on the medial PFC and temporal and parietal cortices, along with ventrolateral PFC (vLPFC) and temporoparietal regions (Svoboda, McKinnon, & Levine, 2006). This pattern overlaps with the default mode network observed at rest (Buckner, Andrews-Hanna, & Schacter, 2008), in accord with the notion that such activity reflects stimulus-independent mental simulations about the self in the past and the future (see below).

PFC Subregions and Memory

Having reviewed overarching PFC contributions to canonical memory processes, we now turn to research on specific PFC subregions: the dLPFC, the vLPFC, the medial PFC (mPFC) and orbitofrontal cortices (OFC), and the rostral or polar PFC. In discussing each sector, we address its differential contributions to the memory processes reviewed above. This parcellation scheme reflects existing frameworks

in the literature, based on functional dissociations and patterns of cortical and subcortical connectivity (Stuss & Alexander, 2007; Tekin & Cummings, 2002). As will be seen below, the divisions reflect dissociations that have been replicated across animal, lesion, and neuroimaging platforms. Yet it is recognized that these divisions of the frontal lobes reflect relative contributions rather than absolute parcellations (Duncan, 2001). Cognitive control, WM, and the subprocesses discussed below—including manipulation, selection, attention, inhibition, encoding and retrieval—“are constructs that have been developed by scientists trying to reverse engineer a highly evolved neurocognitive system . . . they need not correspond to discrete systems that can be meaningfully understood in isolation from the larger system within which they are observed” (Postle, 2011, p. 87).

Dorsolateral PFC

Working Memory

The dlPFC is invariably implicated in WM studies across species. As noted above, the roles of the dlPFC in WM tend to be characterized by higher-order executive control processes, over and above online maintenance of information. For instance, humans with dlPFC lesions exhibit deficits in the ability to manipulate representations in WM, but this impairment is modality-independent and extends to manipulation processes beyond the scope of working memory tasks (Barbey, Koenigs, & Grafman, 2013).

Adaptive behavior in a changing world requires memory not only for perceptual information, but also for contextually appropriate actions. The dlPFC is critical for temporally bridging the gap between perception and appropriate action (“the perception–action cycle”; Fuster, 1997). In addition to stimulus features, the firing rates of dlPFC neurons are tuned to future memory-guided motor responses, and accelerate their firing in anticipation of these responses (Quintana & Fuster, 1999). Neuroimaging evidence suggests that dlPFC activity not only retrospectively codes perceptual sensory information, but also prospectively codes anticipatory action preparation (D’Esposito, Ballard, Zarah, & Aguirre, 2000). Some models of PFC function suggest a superordinate process of integrating

information—both internally and externally generated, retrospective and prospective—across time (Fuster, 2001; Wilson et al., 2010).

Prospective action memory is only adaptive insofar as it is congruent with rules and expected outcomes. In monkeys, delay period activity in lateral PFC neurons codes for reward expectancy (Watanabe, 1990), and even for which particular reward out of several will be received and the manner or magnitude of reward delivery (Leon & Shadlen, 1999; Watanabe, 1996). Individual lateral prefrontal neurons have been found to dynamically code changing task rules (Wallis, Anderson, & Miller, 2001), and to be synchronized to populations of dlPFC neurons that adaptively form coherent rule-selective ensembles oscillating in the beta band (~19–40 Hz) (Buschman, Denovellis, Diogo, Bullock, & Miller, 2012). Beta coherence in local lateral PFC ensembles and distributed networks have been linked to WM-related processes in monkeys (Siegel et al., 2009) and humans (Gross et al., 2004), and interregional beta coherence is associated with top-down neocortical processing more generally (Bressler & Richter, 2014).

The PFC supports complex goal-congruent and rule-based action via selective modulation of task-relevant processes implemented in other brain regions (Miller & Cohen, 2001). It has been argued that delay period activity in the dlPFC mediates the adaptive allocation of attentional resources to posterior perceptual representations and motor plans (Lara & Wallis, 2014; Lebedev, Messinger, Kralik, & Wise, 2004). Consequently, PFC damage has consequences for firing patterns in ipsilesional posterior brain regions, even early visual regions (Barceló, Suwazono, & Knight, 2000). For instance, deactivating the dlPFC via cortical cooling in monkeys and transcranial magnetic stimulation (TMS) in humans attenuates the responsivity of parietal and extrastriate regions and impairs WM performance (Chafee & Goldman-Rakic, 2000; Lee & D’Esposito, 2012). Resting-state functional connectivity as assessed with functional magnetic resonance imaging (fMRI) reveals a “frontoparietal control system,” in which the dlPFC is a functional hub; this system has been linked to cognitive control operations across many task paradigms (Vincent, Kahn, Snyder, Raichle, & Buckner, 2008).

The dlPFC is especially important for sustaining attention to mnemonic content when

distracting information intervenes (Miller, Erickson, & Desimone, 1996; Sakai, Rose, & Passingham, 2002). Some researchers suggest that early observations of impaired delayed-response performance in animals with dlPFC lesions reflect increased susceptibility to interference rather than a failure of short-term retention per se (D'Esposito & Postle, 1999). This suggestion echoes Malmö (1942), who reported that monkeys with frontal lesions could successfully perform the original Jacobson (1936) task if the lights were turned off after cue presentation, concluding that their impairment was one of inhibiting or ignoring extraneous visual stimulation. The dlPFC simultaneously inhibits and attends to perceptual information and internal representations according to task demands. For instance, damage results in a failure of inhibitory modulation of primary sensory cortical activity and excitatory modulation of association cortices during delay periods (Knight, Staines, Swick, & Chao, 1999).

Episodic Memory

The same computational principles associated with the dlPFC in the WM literature apply in the EM literature: The dlPFC is reliably required for manipulating or actively restructuring the contents of consciousness, thereby shaping how they will be encoded and subsequently retrieved. Event-related fMRI studies consistently find increased dlPFC and MTL activity during relational memory encoding and when subsequent memory performance requires retrieving inter-item associations (Blumenfeld, Parks, Yonelinas, & Ranganath, 2011; Qin et al., 2007). Conversely, vlPFC activity supports both item and relational encoding (Blumenfeld, Lee, & D'Esposito, 2014).

We humans often spontaneously adopt strategic organizational strategies when freely recalling information—for instance, by consecutively recalling semantically related items (“semantic clustering”). Neuropsychological research has implicated the PFC in the control mechanisms that support free recall (Stuss et al., 1994), and neuroimaging contrasts between free recall and other retrieval tasks point to the dlPFC as a key region (Staresina & Davachi, 2006). Even dlPFC activity during encoding predicts the degree of semantic clustering during subsequent free recall, whereas

vlPFC activity predicts which words were subsequently recalled, regardless of clustering (Long, Oztekin, & Badre, 2010), supporting the specific role of the dlPFC in actively establishing interitem relations. This finding is consistent with a host of other studies linking dlPFC activity to source memory retrieval (e.g., Dobbins, Foley, Schacter, & Wagner, 2002), which requires relational binding in addition to postretrieval monitoring (Fletcher & Henson, 2001). The dlPFC also subserves top-down modulation of distributed memory networks in memory suppression—another form of memory manipulation. Recent neuroimaging research using fMRI also implicates the dlPFC in goal-directed forgetting, by means of inhibiting hippocampal activity (Benoit, Hulbert, Huddleston, & Anderson, 2015). EEG evidence suggests that the suppression cue triggers alpha (10–14 Hz) phase synchronization in the frontoparietal network (including the dlPFC), which subsequently reduces hippocampal–neocortical coordination, supporting successful suppression (Waldbauser, Bauml, & Hanslmayr, 2015).

Autobiographical Memory

Lateral PFC activation in AM is reduced relative to such activation in laboratory-based episodic memory tasks (Gilboa, 2004). This may be due to the greater context overlap in laboratory stimuli than in real-life events, placing greater demands on effortful postretrieval monitoring in order to distinguish targets from lures (King, Hartley, Spiers, Maguire, & Burgess, 2005). Accordingly, patients with dlPFC lesions tend not to show a marked reduction in naturalistic AM recall (Kopelman et al., 1999; Levine, 2004). However, when prospective AM methods are used to harvest less well-rehearsed and preestablished real-life events, dlPFC activation is observed during retrieval (Cabeza et al., 2004; Levine et al., 2004). When AM retrieval is separated into construction and elaboration phases, a frontoparietal network including left dlPFC and dorsal anterior cingulate cortex (dACC) is observed specifically in association with construction (St. Jacques, Kragel, & Rubin, 2011), likely reflecting control processes related to strategic memory search. This network approximates the intrinsic frontoparietal control network that is commonly implicated in WM studies and is linked to adaptive top-down controlled

processes (Vincent et al., 2008), illustrating the dynamic interdependence between ostensibly different memory systems.

The frontoparietal network couples with the default mode network observed during AM (see below) when AM processes are recruited in a goal-directed manner, as in autobiographical planning (Spreng & Schacter, 2012) and simulating future event outcomes (Gerlach, Spreng, Madore, & Schacter, 2014). Behaviorally, WM capacity predicts the extent to which individuals engage in adaptive future thinking and autobiographical planning during mind wandering (Baird, Smallwood, & Schooler, 2011). These studies present AM processes as being fundamentally flexible and adaptive (Schacter et al., 2012), and echo the discussion above about the interplay between lateral PFC-mediated executive processes and representational information in linked to posterior associative cortex.

Ventrolateral PFC

Working Memory

A large portion of the WM literature focuses on the dlPFC or evaluates the lateral surface of the PFC as a whole. The vlPFC, however, is often additionally implicated as a sensory or attentional gateway to the PFC, mediating the selection of goal-relevant information. For instance, monkeys with ventrolateral lesions are unimpaired on delayed-match-to-sample task across varying delay lengths, but are significantly impaired on a simultaneous color-matching task with ostensibly no mnemonic component (Rushworth, Nixon, Eacott, & Passingham, 1997). In electrophysiological studies finding process-specific tuning throughout the dorsal-ventral axis of the lateral PFC, tasks that require gating, biasing, or selecting information (e.g., Wallis et al., 2001; Lebedev et al., 2004) recruit neurons in the ventral aspect to a greater degree. The vlPFC, especially in the right hemisphere, is critical for inhibiting irrelevant activity in posterior regions during memory retrieval (Aron, Robbins, & Poldrack, 2004) and for selecting among simultaneously active representations (see Badre & Wagner, 2007).

These findings are consistent with Petrides's (1994) two-level model, with the vlPFC mediating an initial selection process preceding the actual engagement of short-term memory, and the dlPFC engaged by higher-order processes

such as manipulation and monitoring (see Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997, for neuroimaging evidence). Overall, there is substantial evidence that the vlPFC supports processes that can be characterized as biasing, selection, and inhibition of distributed neural activity in memory and beyond.

Episodic Memory

In line with the aforementioned role of the vlPFC in selection, maintenance, or inhibition in WM, this region is also thought to organize and structure input to the hippocampus, facilitating EM (Moscovitch, 1992; see Simons & Spiers, 2003). Accordingly, many neuroimaging studies of EM encoding find greater vlPFC activity, especially left-lateralized, during subsequently remembered compared to forgotten information (see Paller & Wagner, 2002).

The encoding-related increase in blood oxygenation level-dependent (BOLD) signal in the left vlPFC is accompanied by a local beta-band desynchronization (Hanslmayr et al., 2011). Stimulating and inducing beta (18.7-Hz) resonance (but not other frequency bands) in the vlPFC with TMS during encoding disrupts subsequent free recall (Hanslmayr, Matuschek, & Fellner, 2014), highlighting the contribution of prefrontal neuronal oscillations to the formation of durable memories. Intracranial recordings from human neurosurgical patients suggest that vlPFC activity occurs relatively late during memory formation—after increases in the ventral visual stream and MTL—suggesting that the vlPFC may implement perencoding executive processes, rather than modulating initial hippocampal encoding (Burke et al., 2014).

In addition to memory encoding, the vlPFC is critical for adaptive and goal-relevant memory retrieval. Processes including controlled retrieval and cue specification (Badre & Wagner, 2007) require top-down modulation of long-term stores in cortical association areas, particularly in cognitively effortful situations (Petrides, 2002). Middle and anterior vlPFC activity is observed in tasks that require controlled retrieval, with coactivation in posterior modality-specific cortical regions appropriate to the cued stimulus dimension (Badre & Wagner, 2007), bolstering a process-based view of lateral prefrontal function and calling into question material-specific (semantic and phonological) models of left inferior frontal

cortical function (e.g., Poldrack et al., 1999). The anterior vlPFC also coactivates with the hippocampus and MTL regions during episodic memory retrieval (Simons & Spiers, 2003) and exhibits functional connectivity with an extended ventral pathway—including the anterior temporal cortex, anterior parahippocampal gyrus, and hippocampus—that is modulated by the control demands during retrieval (Barredo, Oztekin, & Badre, 2013). More posterior portions of the vlPFC function after retrieval to select from among automatically retrieved and competing representations (Badre & Wagner, 2007).

Autobiographical Memory

Given the role of the vlPFC in retrieval-related processes like memory search, cue specification, and selection, its contribution to AM depends heavily on the structure of the task—especially on whether and how memories are cued by the experimenter. Nonetheless, the vlPFC, especially in the left hemisphere, is ubiquitous in neuroimaging studies of AM (Svoboda et al., 2006). Lateral PFC activity generally tends to be left-lateralized, regardless of cue modality (Denkova, Botzung, Scheiber, & Manning, 2006), presumably reflecting semantic and verbal processes in autobiographical retrieval. However, these processes may be specific to the search period, whereas subsequent online reexperiencing may instead engage mostly right-lateralized frontal regions (Conway, Pleydell-Pearce, Whitecross, & Sharpe, 2002). Experiments using fMRI and intracranial recordings in humans found left vlPFC and MTL activity specific to personal episodic (but not semantic) autobiographical retrieval (Levine et al., 2004; Steinvorth, Wang, Ulbert, Schomer, & Halgren, 2010), highlighting the contribution of coordinated vlPFC–MTL interactions in detailed autobiographical recollection. Consistent with age-related reductions in detailed episodic autobiographical retrieval (Levine et al., 2002), older adults exhibit relatively reduced top-down modulation of the hippocampus by the vlPFC during AM retrieval (St. Jacques, Rubin, & Cabeza, 2012). Together, these studies suggest that the left vlPFC may mediate elaborative processes or iterative self-cueing during extended narrative recall (Conway & Pleydell-Pearce, 2000), supporting the feeling of mental time travel (Tulving, 2002).

Medial PFC

Working Memory

Across different neuroimaging studies of WM, the posterior portions of the dorsomedial frontal lobes and dorsal anterior cingulate (dACC; ~BA 24) are reliably recruited, often in concert with lateral PFC regions (Duncan & Owen, 2000; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004). Activity in this region is often interpreted as reflecting relative increases in effort, the allocation and “energization” of attention, or executive attentional processes more generally (see Stuss & Alexander, 2007). Damage to dACC in humans impairs memory for action–value associations (Camille, Tsuchida, & Fellows, 2011), and consequently elicits high false-alarm rates in WM (Tsuchida & Fellows, 2009). This is consistent with theories that link dACC function to monitoring response conflict (e.g., Botnick, Cohen, & Carter, 2004).

The mPFC in the rodent has long been linked to navigation and spatial WM functions, based on observations of impaired spatial learning in rodents with mPFC lesions (Kolb, Buhrmann, McDonald, & Sutherland, 1994). It receives direct afferent input from the hippocampus and connects reciprocally to the hippocampus via the thalamus and entorhinal cortex (Jay & Witter, 1991; Xu & Sudhof, 2013). Medial prefrontal–hippocampal interactions in WM performance are facilitated by synchronized oscillatory activity in the theta band (~3–8 Hz) across these two regions (for a review, see Colgin, 2011). Hippocampal–prefrontal theta coherence is likely to be mediated by thalamic connectivity either through anterior thalamic nuclei (Ketz, Jensen, & O’Reilly, 2015) or through the nucleus reuniens in the thalamic midline (Xu & Sudhof, 2013). Rodent models of schizophrenia produce working memory impairments accompanied by reductions in hippocampal–prefrontal theta coherence (Sigurdsson, Stark, Karayiorgou, Gogos, & Gordon, 2010).

Hippocampal–mPFC coordination often exhibits strong relationships with behavior. The phase of hippocampal theta oscillations modulates the firing of large proportions of mPFC neurons during WM, and the degree and distribution of this theta phase entrainment reflect memory accuracy independently of absolute firing rate (Hyman, Zilli, Paley, & Hasselmo, 2010). Theta phase entrainment in the mPFC is also dynamically modulated

by changing contextual cues (Hyman, Zilli, Paley, & Hasselmo, 2005) and is greatest just before decision points in navigation-based WM tasks (Jones & Wilson, 2005), consistent with research linking the mPFC to reward-guided learning and decision making across species (Rushworth, Noonan, Boorman, Walton, & Behrens, 2011). mPFC activity may adaptively code ongoing action–value contingencies, relying on dynamic coordination via theta coherence with the hippocampus, allowing for the coordination of spatial mnemonic and decision-making processes (Jones & Wilson, 2005). In human scalp electroencephalography (EEG), frontal midline theta activity, which is thought to be generated by the mPFC (Ishii et al., 1999), is observed across many task paradigms, with and without explicit spatial components. It is thought to be a signature of neural integration in the service of adaptive action selection (see Hsieh & Ranganath, 2014; Cavanagh & Frank, 2014).

The ventral portions of the mPFC (e.g., BA 10, 24, 25, and 32) and orbitofrontal cortex (OFC; BA 11, BA 47, and the ventral aspect of BA 10) are sometimes considered as a unit or labeled interchangeably (Ongur & Price, 2000; Szczepanski & Knight, 2014). They are both highly interconnected with limbic structures and are linked to reward- and emotion-based decision making (Bechara, Damasio, & Damasio, 2000). However, anatomical investigations suggest that they constitute distinct networks (Ongur & Price, 2000), and experimental evidence suggests they make different contributions to memory. Whereas the mPFC has extensive efferent visceromotor connections, perhaps explaining its contributions to spatial memory, the OFC receives massive input from all sensory modalities (Ongur & Price, 2000; Kringelbach & Rolls, 2004). OFC firing is commonly linked to reward-based and affective aspects of memory (Rosenkilde, Bauer, & Fuster, 2001). In the domain of WM, the medial OFC in particular is critical for the coordination of multiple simultaneous executive operations—for example, the joint maintenance, monitoring, and manipulation of information (Barbey, Koenigs, & Grafman, 2011). The OFC may establish an overall task state abstracted from multisensory, visceral–emotional, and mnemonic information, providing a scaffold for decision making and reinforcement learning, especially when task states and predicted values are primarily defined by internal mnemonic information as opposed

to external perceptual information (Wilson, Takahashi, Schoenbaum, & Niv, 2014).

Episodic Memory

Interactions between the hippocampus and the PFC are thought to support systems consolidation over time and the subsequent retrieval of remote memories (Winocur & Moscovitch, 2011), but recent research demonstrates that early encoding-stage hippocampal–mPFC interactions are also critical for EM. Bero and colleagues (2014) found that contextual learning elicits rapid structural and functional plasticity in mPFC circuits, and that optogenetically silencing mPFC neurons at the time of encoding inhibits activity in the canonical entorhinal–hippocampal circuit and impairs memory formation. This is in line with the idea that mPFC neurons are “tagged” at or near the time of encoding to facilitate cellular-level changes in hippocampal–neocortical networks and establish enduring distributed associative memory traces (Lesburguères et al., 2011; Tse et al., 2011). Hippocampal projections to the mPFC come specifically from the anterior (ventral in rodents) portion of the hippocampus that codes global contextual features of environments, including additional nonspatial contextual features like vestibular feedback, odor, emotional context, and motivational context, compared to the fine-grained spatial coding in posterior hippocampus (Pennartz, Ito, Verschure, Battaglia, & Robbins, 2011; Poppenk, Evensmoen, Moscovitch, & Nadel, 2013). Information flows in the other direction as well: mPFC lesions selectively disrupt hippocampal representations of rule-guided object–location associations, but leave hippocampal spatial firing patterns intact (Nava-wongse & Eichenbaum, 2013). The mPFC may therefore map adaptive actions and affective responses, based on past experience and evaluative feedback signals from motivation- and value-processing regions, onto hippocampal context representations (Euston, Gruber, & McNaughton, 2012).

The mPFC is structurally and functionally connected with a network of regions constituting a canonical recollection network, topographically overlapping with the autobiographical memory network, including the hippocampus, parahippocampal gyrus, posterior cingulate cortex, and retrosplenial cortex (Aggleton, 2012; Rugg & Vilberg, 2012). In fMRI studies of episodic memory

or contextual memory, the left dlPFC, vlPFC, and rostralateral PFC exhibit significant increased activity during objectively correct recollection, but subjective experience of recollection tends to recruit the medial anterior PFC (Spaniol et al., 2009). Evidence from magnetoencephalography (MEG) and intracranial recordings in humans indicates that that oscillatory coherence in the theta band dynamically integrates activity in the mPFC, hippocampus, and distributed cortical regions during recollective retrieval processes such as source memory (Guderian & Düzel, 2005), free recall (Anderson, Rajagovindan, Ghacibeh, Meador, & Ding, 2010), and spatial route memory (Kaplan, Bush, Bonnefond, & Peter, 2014).

The OFC is densely interconnected with the medial temporal lobes (see Ongur & Price, 2000; Kringelbach & Rolls, 2004). Accordingly, bilateral lesions of the OFC have been shown to produce associative memory impairments in primates (e.g., Meunier, Bachevalier, & Mishkin, 1997). Although fMRI studies of the OFC can be hindered by susceptibility artifacts, neuroimaging and neuropsychological findings suggest that OFC is functionally important for episodic encoding, especially for temporal context information (Frey & Petrides, 2000; Duarte, Henson, Knight, Emory, & Graham, 2010). This region is also strongly interconnected with the amygdala, and therefore contributes to EM and AM for affectively salient material (e.g., Markowitsch, Vandekerckhove, Lanfermann, & Russ, 2003).

Autobiographical Memory

In neuroimaging studies of AM, the mPFC invariably exhibits significant increases in activity. Indeed, activation in this region distinguishes AM from laboratory memory tasks (Gilboa, 2004; McDermott et al., 2009). The mPFC is reliably associated with self-referential information processing (Gusnard, Akbudak, Shulman, & Raichle, 2001). Levine, Svoboda, Turner, Mandic, and Mackey (2009) reported on patient M. L., with isolated retrograde amnesia, who performed normally on objective episodic memory tasks but reported reduced subjective recollection and a subjective disconnection to the products of anterograde learning and memory. Evocative memory cues elicited significantly less mPFC activity in M. L. than in controls. Recent evidence suggests that, unlike patients with hippocampal

damage, patients with mPFC damage are able to retrieve and construct detailed events, but are impaired in their ability to incorporate a sense of self into these events (Kurzcek et al., 2015).

The mPFC is a critical structural and functional hub in a distributed set of brain regions labelled the “default mode network,” which exhibits increased functional connectivity during the resting state (Raichle et al., 2001; Greicius et al., 2003) and overlaps considerably with the canonical AM network. This network has also been linked to other immersive and simulative processes, such as mind wandering, imagining future events, navigation, and social cognition (see Schacter et al., 2012), and it is compromised in neurological and psychiatric disorders (Buckner et al., 2008). The mPFC may orchestrate activity in this network in the service of generating self-referential simulations.

Different functional neuroimaging techniques have enriched our understanding of the role of the mPFC in AM. For instance, in an fMRI experiment, Levine and colleagues (2004) richly cued personal episodic memories by using participants’ own audio recordings about past experiences, and they found greater left anteromedial PFC activity compared to personal semantic and nonpersonal memory conditions. Network analyses of protracted AM retrieval find a distributed network, including the hippocampus, that is driven by mPFC activity and is sustained over the course of memory reconstruction and elaboration (St. Jacques et al., 2011; McCormick, St-Laurent, Ty, Valiante, & McAndrews, 2015). Increased mPFC activity in these studies may reflect greater engagement by cues invoking the episodic “self in subjective time” (Tulving, 2002) relative to context-independent semantic memory. In line with this notion, functional connectivity between the medial PFC and hippocampus tracks the vividness of reexperiencing in autobiographical retrieval (Sheldon & Levine, 2013). Fuentemilla, Barnes, Düzel, and Levine (2014) identified a potential mechanism for coordinated mPFC–hippocampal firing during retrieval, finding that vividness and mental imagery ratings during episodic AM were correlated with theta phase synchronization among the mPFC, hippocampus, and precuneus. The fact that mPFC–hippocampal theta phase coherence is often observed during navigation in rodents and during episodic AM in humans supports speculation that human

mnemonic reexperiencing relies on neural circuits evolved for spatial memory (Buzsáki & Moser, 2013). Medial prefrontal theta alterations may also be critical in pathological memory function: Observed increases in resting-state theta oscillations in the mPFC in patients with early-stage Alzheimer's disease have been suggested to compensate for structural damage concentrated in temporoparietal regions (Montez et al., 2009).

The term "ventromedial PFC" (vmPFC) usually refers to the medial orbitofrontal, medial polar, and ventral anterior cingulate regions (Nieuwenhuis & Takashima, 2011). It has been widely researched for its link to confabulation, or the unintentional recollection of erroneous memories without awareness of their falsehood (Moscovitch, 1989). Damage to the vmPFC is sufficient to cause confabulation (Gilboa & Moscovitch, 2002). Models of confabulation posit that it is due to impaired strategic processes during search, retrieval, and postretrieval monitoring (Burgess & Shallice, 1996; Gilboa et al., 2006) accompanied by disinhibition, lack of self-monitoring, and decreased awareness (e.g., Schnider, von Daniken, & Gutbrod, 1996). Laboratory-based memory tasks tend to find that patients with vmPFC damage produce elevated false alarms but normal hit rates (Gilboa et al., 2006), and that confabulation-type errors in neuroimaging studies with healthy participants are linked to transient reductions in vmPFC activity (Turner, Simons, Gilbert, Frith, & Burgess, 2008). A recent model of confabulation draws a link to another process mediated by the vmPFC: the formation and implementation of schemas, or "adaptable associative networks of knowledge extracted over multiple similar experiences" (Ghosh, Moscovitch, Melo Colella, & Gilboa, 2014). Research in rats (e.g., Tse et al., 2011) and humans (e.g., van Kesteren, Rijpkema, Ruiter, & Fernández, 2010) suggests that the vmPFC is critical for schema-supported memory encoding, retention, and retrieval. It may be involved in activating schema-relevant cues during search or monitoring the consistency of retrieved information with respect to existing schemas (Burgess & Shallice, 1996; Gilboa et al., 2006). Schemas—like attention, goals, rules, and prospective actions—present another means by which the PFC modulates and integrates ongoing activity throughout the brain to facilitate adaptive memory-guided action.

AM dynamics include structural and functional changes over seconds, days, weeks and years. The vmPFC is involved in memory consolidation over time, consistent with its role in schema formation. Schemas are a critical component of AM: Day-to-day episodes are experienced and remembered according to similar, preexisting, distributed networks of knowledge (Ghosh et al., 2014). The hippocampus is a critical hub of memory retrieval, insofar as rich context-specific details are retained (Nadel & Moscovitch, 1997; Sheldon & Levine, 2013); with time and repeated reactivation, however, hippocampus-dependent memory traces become more dependent on extrahippocampal cortical connections, and memories become correspondingly more gist-like and skeletal (Alvarez & Squire, 1994; Nadel & Moscovitch, 1997; Winocur & Moscovitch, 2011). Recent research suggests that the vmPFC, which is densely connected with the hippocampus, becomes a cortical hub for consolidated memories by extracting regularities across episodes and integrating memories into preexisting schemas (for a review, see Nieuwenhuis & Takashima, 2011).

Theories of the cellular mechanisms of consolidation suggest that it is supported by the coordinated replay of memories in the hippocampus and mPFC (Colgin, 2011). During sleep, neurons in the rodent infralimbic cortex—a potential homologue for the human vmPFC—exhibit repeated reactivation of cellular firing sequences observed during recent waking experience (Nieuwenhuis & Takashima, 2011). There is evidence that this replay is coordinated via oscillatory interactions with the hippocampus and is predictive of memory stability over time (Gais et al., 2007). Furthermore, medial prefrontal replay during sleep is primarily observed in cell ensembles for which firing was phase-aligned with hippocampal theta oscillations during initial learning and decision making (Benchenane et al., 2010). Consistent with rodent models of the vmPFC's role in systems consolidation, human neuroimaging evidence suggests that the vmPFC instantiates representations of remote memories more than recent memories and more than any other individual brain region (Bonnici et al., 2012). Thus, in addition to implementing cognitive control operations, the vmPFC may be a hub for remote autobiographical information as a result of interplay with the hippocampus over time.

Frontopolar Cortex

Working Memory

Several models of PFC functional organization suggest a caudal-to-rostral axis of increasing computational abstraction (Christoff & Gabrieli, 2000; Badre & D'Esposito, 2009). The frontopolar cortex, or rostral PFC (BA 10), is located at the top of this hierarchy, and is disproportionately enlarged and interconnected in humans relative to nonhuman animals (Burgess, Dumontheil, & Gilbert, 2007; Semendeferi et al., 2011). Models of rostral PFC function highlight the importance of this region in integrating external (perceptual) and internal (goal-directed and representational) signals (Fuster, 2009), and in acting as a gateway between them (Burgess et al., 2007). It is unsurprising, therefore, that the rostral PFC exhibits changes in functional brain activity across myriad memory tasks and paradigms (Burgess et al., 2007). However, patients with damage in this region are typically selectively impaired on tasks that require multitasking, or “prospective memory”—remembering to execute delayed intentions at appropriate times in the face of distraction (Volle, Gonen-Yaacovi, Costello, Gilbert, & Burgess, 2011). There is neuropsychological and neuroimaging evidence that the rostral PFC utilizes cues for the timely enactment of prospective intentions, rather than representing them per se (Uretzky & Gilboa, 2010; Gilbert, 2011). This is in line with previous work emphasizing the role of the frontopolar cortex in aligning hierarchical relationships among subprocesses toward the current overall goal—for instance, “cognitive branching” (Koechlin, Basso, Pietrini, Panzer, & Grafman, 1999) and “goal–subgoal integration” (Braver & Bongiolatti, 2002).

Episodic Memory

The frontopolar region is critical for long-term episodic and associative memory, with lesions in this region affecting the ability to reexperience the past (Wheeler & Stuss, 2003). This finding is echoed in the early neuroimaging literature on memory (see Grady, 1999). Later formulations of frontopolar function emphasized the evaluation of internally generated states and events (Christoff & Gabrieli, 2000), particularly for the medial polar region (Simons, Owen, Fletcher, & Burgess, 2005). Other models emphasize a temporally

sustained “retrieval mode” that biases or gates upstream activity (Tulving, 1983; Velanova et al., 2003), which holds for encoding operations as well: Sustained rostrolateral contextual representations serve to integrate items in close temporal context during memory formation (Jenkins & Ranganath, 2010). These models are consistent with the hierarchical view of PFC organization noted above (Badre & D'Esposito, 2009). In our focal lesion sample, frontopolar and medial PFC lesions are associated with elevated production of external (nonepisodic) details during AM recall, whereas internal (episodic) details are intact (Levine et al., in preparation). This finding is interpreted as reflecting impaired evaluation of mnemonic output with respect to internally focused retrieval.

Summary and Conclusions

This chapter presents an overarching view of the PFC as implementing dynamic and adaptive cognitive control operations, biasing and integrating neural activity in distributed brain regions in the service of memory and memory-guided behavior. We have outlined general principles characterizing PFC functional contributions to WM, EM, and AM tasks. We have also outlined the function of specific subregions—dorsolateral and ventrolateral, medial and orbitofrontal, and frontopolar cortices—in the different sections of the memory literature, with an emphasis on component processes cutting across task distinctions. There is converging evidence from anatomical, neuropsychological, and neuroimaging research supporting these functional–anatomical dissociations in the PFC. However, contemporary research suggests that a hallmark of PFC activity is its distributed and flexible nature, and that functional dissociations within the PFC probably do not reflect discrete computations performed locally, but rather distinct functional hubs in distributed domain-general networks. Plate 9.1 illustrates the overlap between functional brain networks observed in particular memory tasks and intrinsic, domain-general networks observed in the resting state discussed throughout this chapter.

In memory studies using electrophysiological recordings in animals, many neurons develop selective responses to one or another element

of the experiment over the course of training, and the response tuning of individual neurons depends strongly on the selection criteria. For example, at lower thresholds, feature-specific tuning is observed throughout the lateral PFC, and relatively few neurons in any one region are robustly tuned to one specific element across studies (Duncan, 2001; Scalaidhe, Wilson, & Goldman-Rakic, 1999). Furthermore, recent advances in analytical tools have revealed that prefrontal neurons go through multiple representational states over the course of cue presentation, delay, and behavioral response within a given trial (Stokes et al., 2013), and that task demands (e.g., recognition vs. recall) can be decoded from the covariance of the whole population of recorded neurons even when no individual neurons exhibit detectable selectivity (Rigotti et al., 2013). These studies jointly suggest that the functional organization of memory-related processes in the PFC is dynamic, flexible, and distributed, and that these properties emerge from interactions between “mixed selective, adaptive coding, multifunctional” neurons (Miller, 2013).

Descriptions of overarching PFC functions employed throughout this chapter, such as “top-down modulation” and “cognitive control,” can amount to a biologically implausible, homunculus-like model of the PFC in memory and cognition (Hazy, Frank, & O’Reilly, 2006; Fuster, 2009). Rather, we and others argue that complex memory function emerges out of reciprocal brainwide interactions at multiple time scales (Fuster & Bressler, 2012; Hasson, Chen, & Honey, 2015), but that the unique connectivity profile of the PFC and its place in the processing hierarchy give it particular importance in adaptively constraining these interactions. Oscillatory coherence within and across frequency bands, and within and across cell populations, presents a likely mechanism for coordinating distributed activity in transient memory networks (Düzel, Penny, & Burgess, 2010; Bressler & Richter, 2014), allowing for sustained WM operations in the absence of external input and for (re)constructing rich and coherent episodes in episodic and autobiographical memory.

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