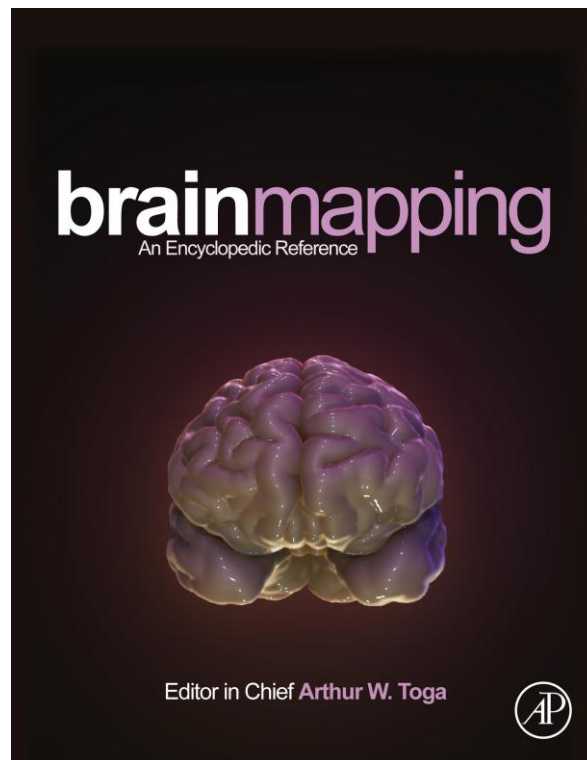


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Nee D.E., and D'Esposito M. (2015) Working Memory. In: Arthur W. Toga, editor. *Brain Mapping: An Encyclopedic Reference*, vol. 2, pp. 589-595. Academic Press: Elsevier.

Working Memory

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Glossary

Caudal In the brain, caudal areas are posterior or close to the back of the head.

Dorsal In the brain, dorsal areas are superior or closer to the top of the head.

fMRI Functional magnetic resonance imaging; a form of imaging that measures magnetic properties of blood-oxygen.

PET Positron emission tomography; a form of imaging that uses a radioactive tracer to examine metabolic activity.

Rostral In the brain, rostral areas are anterior or closer to the nose.

Ventral In the brain, ventral areas are inferior or closer to the neck.

Introduction

Consider the process of crossing a busy street. Following the adage 'look both ways,' you may begin by looking right, noting vehicle types (e.g., car, truck, and bicycle), observing their approximate speed, and estimating the time at which each vehicle will cross your path. Then, you may look to the left and repeat the process. As you do so, it is essential that information gathered from the initial look to the right is not lost. If information about the recent past cannot be maintained, one would endlessly vacillate right and left, gathering information and losing it. Fortunately, our cognitive system has been tuned to keep track of recent events, recognizing the likelihood that recent information has bearing upon future cognition. The system responsible for the maintenance of recent information that is no longer available to the senses is called working memory. Working memory forms a temporal bridge that links the recent past to the present.

Working memory is generally thought to consist of two sub-components. First, information must be codified such that relevant features are stored for future use. For example, when preparing to cross a street, one will initially perceive a number of aspects of an oncoming car such as its color, make, speed, and location. For the purpose of crossing the street, features that will allow you to avoid the car (e.g., speed and location) will be stored in working memory while features irrelevant to this goal (e.g., color and make) will likely be discarded. Second, stored information must be kept active. This involves a process that rehearses or refreshes the stored representation to preserve its fidelity over time. The term 'working memory' implies a single, cohesive system involved in the temporary maintenance of information. However, working memory is better thought of as a function (i.e., to maintain information), which is then characterized by the content (i.e., what is maintained). Just as there are different areas of the cortex responsible for the processing and representation of different types of content, so too are there different systems involved in the maintenance of different types of content (Courtney, 2004; Curtis & D'Esposito, 2003; Jonides, Lacey, & Nee, 2005; Postle, 2006). The best-studied working memory systems are those that maintain verbal content (e.g., words and letters), spatial content (e.g., egocentric position), and visual-object content (e.g., faces). We begin by considering the working memory systems responsible for the maintenance of each of these forms of content and then generalize the principles for understanding working memory of all forms of content. We

follow by discussing how each of these systems is coordinated through control processes, which are themselves dictated by context. We close with a simple model framework that ties together working memory and its control.

Verbal Working Memory

Much of the study of working memory can trace its routes back to the research of Baddeley and colleagues (Baddeley, 1986; Baddeley & Hitch, 1974). Baddeley's phonological loop model of the verbal working memory system remains the dominant model to this day. The phonological loop model assumes that the primary representation for verbal information is phonological. Evidence for this claim comes from observations that, in tests of verbal working memory, erroneously recalled items are often phonologically similar to the true test items (Conrad & Hull, 1964). This phonological similarity effect suggests not only that verbal items are stored using a phonological code but also that forgetting occurs at the level of individual speech sounds or phonemes. Thus, the storage component of the model, the phonological store, is assumed to represent verbal content as sets of phonemes, which rapidly decay causing forgetting. To maintain its fidelity, information held in the phonological store can be refreshed through articulatory rehearsal involving subvocalization (i.e., inner speech). By looping articulatory rehearsal, information in the phonological store is kept active. Importantly, articulatory rehearsal is only effective if it outpaces the rate of decay from the phonological store.

The concept of the phonological loop shares close ties to language functions. Phonological representation is common to both verbal working memory and speech perception, suggesting potentially common mechanisms. Furthermore, articulatory rehearsal corresponds closely to speech production. As a result, one might expect the phonological store to be localized in the left perisylvian areas involved in speech perception (i.e., Wernicke's area; areas 40, 39, and 22) and articulatory rehearsal to be localized in the left inferior frontal areas involved in speech production (i.e., Broca's area; areas 44 and 45; see Figure 1 for the localization of relevant brain areas throughout). Neuroimaging data first using PET (Awh et al., 1996; Fiez et al., 1996; Jonides et al., 1997; Paulesu, Frith, & Frackowiak, 1993; Smith, Jonides, & Koeppe, 1996) and then using fMRI (Braver et al., 1997; Chein & Fiez, 2001; Cohen et al., 1997) have been broadly consistent

pushed the neural locus of spatial working memory dorsally in the human cortex. Courtney, Petit, Maisog, Ungerleider, and Haxby (1998) tested this hypothesis by directly comparing spatial and object working memory in the same subjects. These authors found that an area in the superior frontal sulcus (SFS; area 8) demonstrated sustained activation during the delay period of a spatial working memory task and that this activation was significantly greater for spatial working memory as compared with object working memory. This result has now been replicated numerous times (see Rottschy et al., 2012, for a recent meta-analysis). By contrast, area 9/46 was sensitive to both object working memory and spatial working memory. This result indicated that human area 9/46 is more domain-general than had been anticipated by the monkey data (see control of working memory later in the text). For clarity, we will henceforth refer to areas 46 and 9/46 as mid-lateral PFC to distinguish them from the SFS (area 8) and avoid confusion with the term 'DLPFC,' which has been used to refer to all of these areas in the monkey.

The SFS is adjacent to areas that control both eye movements and covert attention known as the frontal eye fields. It is widely accepted that areas involved in spatial working memory are closely related to those involved in eye movements and covert attention (Awh & Jonides, 2001; Awh et al., 1999; Corbetta, Kincade, & Shulman, 2002). Thus, just as areas involved in articulatory rehearsal in verbal working memory are closely related to speech production, the areas involved in rehearsal in spatial working memory are likely to be closely related to eye movements. This commonality suggests that our capacity to rehearse information in working memory has evolved closely from capacities to direct motor movements (Buchsbbaum & D'Esposito, 2008b).

In addition to the SFS, human spatial working memory also consistently engages the PPC (areas 7 and 40) (Courtney et al., 1998; Curtis, Rao, & D'Esposito, 2004; Jonides et al., 1993; Leung, Gore, & Goldman-Rakic, 2002; Rottschy et al., 2012; Smith et al., 1996; Sweeney et al., 1996; Wager & Smith, 2003). Furthermore, activations in the PPC are topographically organized such that different parts of the PPC respond to different parts of space (Schluppeck, Glimcher, & Heeger, 2005; Sereno, Pitzalis, & Martinez, 2001; Silver, Ress, & Heeger, 2005). Activations in topographically organized areas of the PPC are sustained during spatial working memory maintenance (Schluppeck, Curtis, Glimcher, & Heeger, 2006). These data suggest that the PPC represents a map of space that is held online in the service of working memory. This idea is consistent with evidence of location-specific sustained firing in monkey PPC (Chafee & Goldman-Rakic, 1998; Constantinidis & Steinmetz, 1996). Together, the data suggest that the SFS stores a prospective motor code while the PPC maintains a representation of visual space (Curtis et al., 2004). Furthermore, activations between the SFS and PPC are strongly correlated (Fox, Corbetta, Snyder, Vincent, & Raichle, 2006; Power et al., 2011; Shirer et al., 2012), suggesting a high degree of interaction to support spatial functions.

Object Working Memory

As in spatial working memory, the neural basis of human object working memory was anticipated by data from monkeys

that suggested that the VLPFC (Fuster, Bauer, & Jervey, 1982; Miller, Erickson, & Desimone, 1996; Mishkin & Manning, 1978; Mishkin, Vest, Waxler, & Rosvold, 1969; Rao, Rainer, & Miller, 1997; Wilson, Scialidhe, & Goldman-Rakic, 1993) and temporal cortex (Fuster, 1990; Fuster, Bauer, & Jervey, 1981; Fuster & Jervey, 1982; Horel, Pytko-Joiner, Voytko, & Salisbury, 1987; Horel, Voytko, & Salisbury, 1984; Mishkin, 1982; Miyashita & Chang, 1988; Nakamura & Kubota, 1995; Petrides, 2000) are critical neural loci for object working memory. Human neuroimaging data have localized homologous areas of the VLPFC and temporal cortex for object working memory. As mentioned previously, Courtney et al. (1998) found that dorsal frontal areas in the SFS were preferentially recruited for spatial working memory as compared with object working memory. The reverse (i.e., object working memory > spatial working memory) was true in the VLPFC (area 45). This dorsal/ventral distinction in the PFC has been replicated numerous times in direct comparisons between spatial working memory and object working memory (Courtney, Ungerleider, Keil, & Haxby, 1996; Mohr, Goebel, & Linden, 2006; Munk et al., 2002; Sala & Courtney, 2007; Sala, Rama, & Courtney, 2003), as well as in meta-analyses of neuroimaging data (Nee et al., 2013; Owen, McMillan, Laird, & Bullmore, 2005; Rottschy et al., 2012). Dorsal/ventral distinctions between spatial working memory and object working memory have also been observed in posterior cortices (Courtney et al., 1996; Postle & D'Esposito, 1999; Postle, Stern, Rosen, & Corkin, 2000; Sala et al., 2003; Smith et al., 1995), which have been confirmed in meta-analyses (Rottschy et al., 2012; Wager & Smith, 2003). Collectively, these data indicate that a VLPFC-temporal network underlies human object working memory.

A common strategy for examining object working memory within neuroimaging in humans is to interrogate areas of the brain specialized for processing particular object types. One salient example is a region of temporal cortex that preferentially processes faces often referred to as the fusiform face area (FFA) (Kanwisher, McDermott, & Chun, 1997). Studies have used perceptual tasks that contrast the processing of faces with the processing of other kinds of objects (e.g., houses) to functionally localize the FFA. Then, FFA responses are examined during delay intervals while faces are maintained in working memory. Using this strategy, it has been observed that the FFA demonstrates persistent activation during delay periods (Druzgal & D'Esposito, 2001; Lepsien & Nobre, 2007; Ranganath, DeGutis, & D'Esposito, 2004; Sala et al., 2003). Furthermore, delay-period FFA activation is positively modulated by the number of faces held in object working memory, suggesting that its activity is a linear function of working memory load (Druzgal & D'Esposito, 2001, 2003). Moreover, working memory activation in the FFA can occur independently of the presentation of faces. When participants learn to associate nonface cues with face stimuli for a delayed paired association decision, presentation of the nonface cue elicits delay-period activation in the FFA (Ranganath, Cohen, Dam, & D'Esposito, 2004a). Furthermore, when faces are held in working memory, activation in the FFA is strongly correlated with the VLPFC (Gazzaley, Rissman, & D'Esposito, 2004), suggesting that interactions between these areas support working memory for faces. Finally, these observations are not exclusive to the FFA. For example, areas of temporal

cortex that represent scenes show scene-specific working memory effects (Lepsien & Nobre, 2007; Ranganath, DeGutis, & D'Esposito, 2004). Together, these data indicate that the same areas of the brain that process categorical object information in perception retain that information for the service of working memory.

Working Memory: Emergent System View

The data reviewed in the preceding text indicate that each working memory system consists of a frontal–posterior interaction. For each system, information represented in posterior cortical areas is maintained through the functions of frontal areas that project to them. Phonological information represented in perisylvian cortex is maintained through articulatory rehearsal processes of Broca's area. Spatial information represented in PPC is maintained through spatial attention processes of the SFS. Object information represented in the temporal cortex is maintained through top-down biasing from the VLPFC. In general, the working memory of any form of content can be thought of as the representation of that content and the selection of that content to keep it active/protected. The representation of content is shared with the perceptual system. The selection of content can be thought of as synonymous with attention (Desimone & Duncan, 1995). In this way, working memory emerges from functions of perception (representation) and attention (selection; Courtney, 2004; D'Esposito, 2007; Jonides et al., 2005; Postle, 2006).

Control of Working Memory

As reviewed earlier in the text, research by Goldman-Rakic and others led to substantial interest in the midlateral PFC as an important neural substrate of working memory, particularly in the spatial domain. However, human neuroimaging research revealed that the midlateral PFC (areas 9/46 and 46) performs a more domain-general function than had been originally anticipated (D'Esposito et al., 1998). The midlateral PFC is active when the contents of working memory are reorganized (Barde & Thompson-Schill, 2002; D'Esposito, Postle, Ballard, & Lease, 1999; Postle et al., 1999; Wagner, Maril, Bjork, & Schacter, 2001) and used to direct behavior (Pochon et al., 2001; Rowe, Toni, Josephs, Frackowiak, & Passingham, 2000) and when multiple working memory systems are coordinated (D'Esposito et al., 1995). In contrast to posterior cortical areas that show rigid specializations for particular features, heterogeneous activity in the midlateral PFC confers a vast representational repertoire (Rigotti et al., 2013), enabling the ability to adapt representations to changing environmental demands (Stokes et al., 2013). Generally, the midlateral PFC is consistently involved when behaviors are based upon an internally guided state (Miller & Cohen, 2001). In this way, the midlateral PFC can be considered to represent and maintain rules for goal-directed behavior. The representation of rules is necessary when the information available from the environment alone does not indicate the appropriate behavior. Consistent with these data, rule-selective neurons have been identified in

the monkey midlateral PFC (Asaad, Rainer, & Miller, 1998, 2000; Wallis, Anderson, & Miller, 2001; Wallis & Miller, 2003), and individual rules can be identified based upon patterns of fMRI activation in the human midlateral PFC (Nee & Brown, 2012; Woolgar, Thompson, Bor, & Duncan, 2010). These data converge on the idea that the midlateral PFC represents rules that align behavior with internal goals. Such rules can direct and coordinate the activity in working memory systems.

Rules themselves are dictated by contexts. Badre and D'Esposito (2007) compared fMRI activations across tasks that required simple stimulus–response associations, complex stimulus–response associations, and complex stimulus–response associations that varied as a function of context (Figure 3). Compared with simple stimulus–response associations, complex stimulus–response associations required the internal representation of a rule to map the stimulus to the response. Correspondingly, the midlateral PFC was active for the latter, but not for the former. Moreover, when rules varied on a block-by-block basis and were thus contextually bound, the frontopolar cortex (FPC; area 10) became active. Similar rostral–caudal progressions have been observed in other fMRI studies (Koechlin, Ody, & Kounineher, 2003; Nee & Brown, 2012, 2013; Nee, Jahn, & Brown, 2014). These results suggest a hierarchical organization in the PFC such that more caudal areas of the PFC are informed by the representations of rostral areas of the PFC (Badre & D'Esposito, 2009). Recent studies of patients with focal PFC lesions provide causal evidence of these roles and their hierarchical interactions (Azuar et al., 2014; Badre, Hoffman, Cooney, & D'Esposito, 2009). Hence, caudal areas of the PFC involved in working memory maintenance are coordinated by the midlateral PFC, which is informed by the FPC (Badre & D'Esposito, 2009).

Summary and Conclusion

Taken together, the data indicate that working memory is controlled by the PFC. Working memory itself relies on the top-down influence of caudal PFC areas on posterior cortices. Distinct caudal PFC–posterior networks are involved for different kinds of information. The caudal areas of the PFC involved in working memory retention are themselves influenced by the midlateral PFC that represents rules. Rules coordinate the use of information maintained in working memory systems. When rules vary from situation to situation, the rules can be contextualized by the operations of the frontopolar cortex. Collectively, we propose that the organization of the brain with respect to working memory can be conceptualized with a four-layer model (Figure 4). First, working memory is composed of representations that are embodied in activity in posterior cortical areas. Second, posterior activity is maintained through the action of caudal areas of the PFC. Third, caudal areas of the PFC are themselves coordinated and controlled according to currently relevant rules that are represented in the midlateral PFC. Fourth, the currently relevant rule is established by the context represented in the frontopolar cortex. Hence, working memory and its control involve widespread cortical areas from posterior cortices to the rostral-most areas of the PFC.

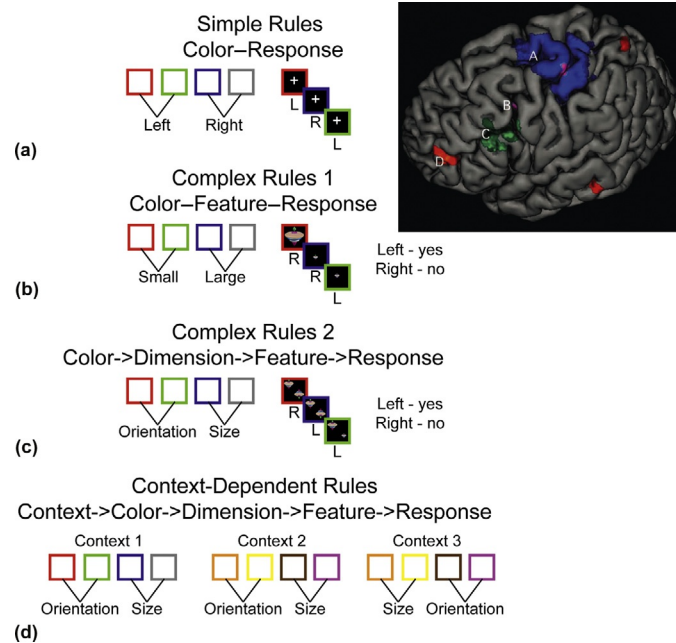


Figure 3 Progression of rule- and context-related activations. Task and data are based upon [Badre and D'Esposito \(2007\)](#). (a) Simple rules map colors to responses and elicit activations in motor and premotor (area 6) cortices. (b) More complex rules map colors to features. For example, red frames indicate that small objects require a 'yes' (left) response. Such rules activate caudal areas in the PFC. (c) Even more complex rules map colors to dimensions. For example, red frames indicate that orientation is the dimension of interest. Thus, if both objects have the same orientation (e.g., both upright), a 'yes' (left) response is required. Such rules activate more rostral areas of the midlateral PFC (area 9/46). (d) Contexts dictate the color-to-dimension mappings. When distinct contexts indicate competing mappings (e.g., context 2 indicates orange-orientation while context 3 indicates orange-size), rules are guided by context with corresponding activations in the FPC (area 10).

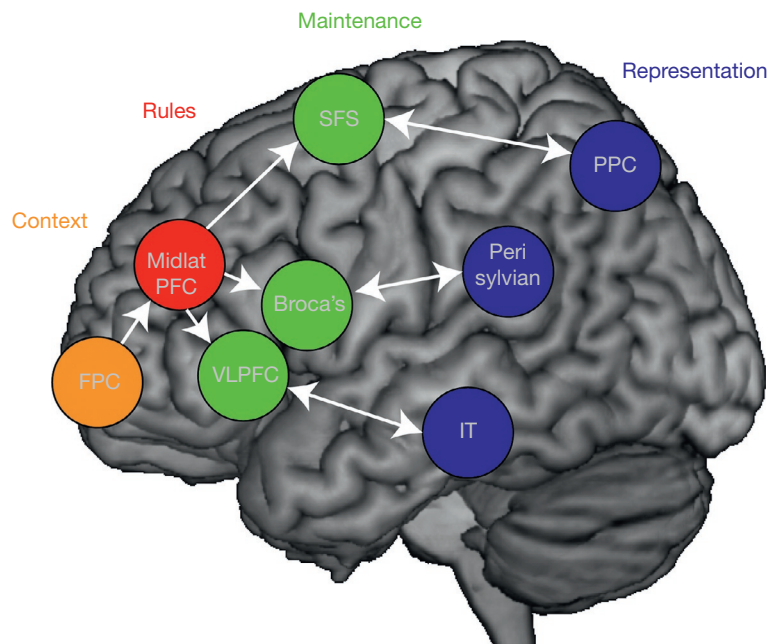


Figure 4 A four-layer model of working memory. Posterior areas are involved in information representation with distinct areas coding for spatial information (PPC), verbal information (perisylvian), and object information (IT). Each of these posterior areas communicates with caudal frontal areas whose interactions form the basis of maintenance. Rules, represented in the midlateral PFC, coordinate what sort of information to maintain (e.g., spatial, verbal, and object) and with what priority, thereby providing control. Rules themselves are guided by contexts represented in the FPC, so that different rules can be applied in different situations.

See also: INTRODUCTION TO ANATOMY AND PHYSIOLOGY: Lateral and Dorsomedial Prefrontal Cortex and the Control of Cognition; Posterior Parietal Cortex: Structural and Functional Diversity; INTRODUCTION TO COGNITIVE NEUROSCIENCE: Attention and Memory; Hierarchical Reinforcement Learning; Memory Attribution and Cognitive Control; Rule Representation; Short-Term Memory; Working Memory; Working Memory–Attention Interplay; INTRODUCTION TO SYSTEMS: Face Perception; Visuospatial Attention.

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