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## Book and new media reviews

# Recent trends in the cognitive neuroscience of working memory

A Review of “The Cognitive Neuroscience of Working Memory” by Naoyuki Osaka, Robert H. Logie, Mark D’Esposito (Eds.), Oxford University Press (2007), Price: £45 (US\$ 89.50), ISBN 0198570392.

*The Cognitive Neuroscience of Working Memory* (CNWM) is an edited volume, inspired by The Second International Conference on Working Memory, which took place in Kyoto, Japan in the summer of 2004. Each of the invited speakers was invited to contribute a chapter for the volume. The upside of this approach is that the book provides the reader with a broad sampling of state-of-the-art research in the field of working memory. The downside is that the volume lacks an overarching set of goals, and many of the chapters are not devoted to the cognitive neuroscience of WM. Yet, despite a lack of coherence, the book succeeds in capturing a number of important themes that are driving contemporary research on WM. The purpose of this review is to highlight some of these themes, and in so doing, to provide a selective overview of the contemporary landscape of WM research. We will also discuss recent computational modelling approaches to WM, which unfortunately were not addressed by the Osaka et al. volume.

Some of the most enjoyable passages in CNWM come from the introductory chapter by Baddeley and Hitch. What makes this chapter special is that Baddeley and Hitch provide an autobiographical account of the circumstances that led to their seminal 1974 chapter on WM. We learn that Baddeley and Hitch came together at Cambridge in 1971 to work on a grant devoted to exploring the relationship between short- and long-term memory (STM and LTM), at a time when the field had largely tired of the topic of STM, and instead had turned to the transfer of information to LTM (e.g., Craik and Lockhart, 1972) and to the organisation of LTM (Collins and Quillian, 1969; Tulving, 1972). At the same time, however, neuropsychological data had demonstrated that patients with severe STM deficits could function normally in everyday life and in many important cognitive activities (Shallice and Warrington, 1970). These data called into question most contemporary models, which assumed that STM served as an essential gateway to the information-processing stream, and re-invigorated Baddeley and Hitch, leading them to investigate the function of STM, i.e., the role that temporary storage might play in higher-order

cognition. It is for this reason that they named their construct *working memory*.<sup>1</sup>

While the opening chapter is a pleasure to read, one cannot help but notice that most of the subsequent chapters do not embrace the Baddeley model (in fact, some provide a compelling account for its demise; see Marklund and Nyberg, Chapter 18; Postle, Chapter 19). Indeed, the first theme we discuss below is the historical transition from multi-store models of WM to more dynamic, functional approaches. The Osaka et al. volume demonstrates that this transition may be nearly over – many contemporary researchers of WM no longer use the Baddeley model as a framework (but for a dissenting view, see Baddeley, 2007). They choose, instead, to think of WM as the active portion of LTM, coupled with mechanisms for cognitive control. It is, perhaps, ironic that neuroscience data (e.g., Shallice and Warrington, 1970) largely motivated the original Baddeley and Hitch model, yet as we learn later in the volume, such data are currently providing the greatest challenges to the model (e.g., Postle, 2006).

Our review of CNWM will forego a detailed discussion of each individual chapter. Instead, we will focus on a few broad themes that we see running through the volume, and discuss how they correspond to contemporary research in WM, as we see it. Our apologies in advance to the authors of chapters that receive less attention in this review; we do not mean to diminish the contribution of these authors as each chapter is worth the reader’s attention; some chapters simply fit the themes we extracted better than others.

## 1. From multi-store to dynamic models of WM

Many younger scientists in the area of WM, particularly those coming from a neuroscience perspective, have difficulty in understanding the significance of the shift from multi-store models of memory to more dynamic, functional models. Indeed, these younger scientists came to the field after the rise of connectionism, parallel distributed processing, and neuroimaging. However, it is important to remember that

<sup>1</sup> The phrase *working memory* was actually first introduced by Miller et al. (1960), but the Baddeley and Hitch (1974) chapter is widely recognized as the birth of contemporary research on WM.

contemporary models of WM are largely influenced by the multi-store model of [Baddeley and Hitch \(1974\)](#), who were in turn influenced by [Broadbent \(1958\)](#) and the cognitive renaissance of the 1950s, when the mind came to be viewed as an information-processing system, consisting of multiple stores or structures, that transmit information from one to another.

Multi-store models fell out of favour in the 1980s, as communication-channel and computer metaphors of the mind gave way to more biologically plausible systems, such as neural networks. In the area of WM, [Anderson \(1983\)](#) introduced the idea that WM could be modelled as the activated portion of LTM.<sup>2</sup> By this view, LTM representations may be activated to varying degrees by external or internal events, and when that activation reaches a threshold, the information carried by that representation becomes available for further action (and possibly enters consciousness). Similar models of WM were proposed by [Schneider and Detweiler \(1987\)](#) and [Cowan \(1988\)](#), each of which viewed WM as a set of concurrently activated representations, governed by mechanisms associated with cognitive control. Cowan's model is a bit of a hybrid structural/dynamic model in that it retains multiple components or structures, such as the central executive, but it views WM as the activated portion of LTM, which is more consistent with the dynamic approach.

Two chapters in the Osaka et al. volume take a fully dynamic approach and challenge the Baddeley model of WM ([Marklund and Nyberg, Chapter 18](#); [Postle, Chapter 19](#)). According to these authors, neither the processes underlying domain-specific memory representation, nor the mechanisms associated with cognitive control, are *unique* to WM. WM can instead be thought of as an emergent property of the mind, the result of coordinated neural activity among brain regions associated with cognitive control and mnemonic representation. Postle follows up on his influential 2006 review paper, in which he argues that the original multi-store model proposed by Baddeley does not hold up to recent data from neuroscience. In particular, there does not appear to be any evidence for storage buffers, such as the phonological loop or the visuo-spatial sketchpad. Instead, short-term retention of information is achieved “via sustained activity in anatomical networks whose principle function is not mnemonic” ([Postle, Chapter 19](#)).

For example, consider fMRI experiments using the *n*-back task as a measure of WM. Participants see or hear a continuous stream of stimuli, typically once in every 2–3 sec, and must indicate whether the current item matches the one *n*-back in the stream. One nice feature of the *n*-back task is that it affords a wide variety of stimuli, from digits, letters, and words, to faces and abstract shapes. As well, parametric manipulations of *n*-back have been shown to correspond to increases in activity in prefrontal cortex (PFC; [Braver et al., 1997](#)), which is consistent with seminal single-cell recording data in primates demonstrating sustained delay-period activity in PFC neurons during performance of WM tasks (e.g., [Goldman-Rakic, 1987](#); also see [Funahashi, Chapter 13](#)). A central question in fMRI experiments has been whether

there is domain-specific neural activity in PFC, thus suggesting that the PFC is segregated by stimulus domain and responsible for temporary mnemonic representation, or whether the observed activity in PFC is domain-general (perhaps related to attention) and the domain-specific activity comes from more posterior regions associated with the perception of the stimuli being used in the task. [Postle](#) argues for the latter interpretation (see also [Postle, 2006](#)). In particular, he details an experiment designed to separate activity that is correlated with, but not necessary for, the temporary maintenance of information during an *n*-back task ([Postle and D'Esposito, 1999](#)). Three 7 sec delay periods were interposed between the first and second, second and third, and third and fourth stimuli. Several brain regions demonstrated activity in the first delay period, including PFC, posterior fusiform gyrus, and posterior parietal cortex. However, only posterior fusiform gyrus, which previously had been shown to be involved in the perception of faces, demonstrated activity throughout all the delay periods. Based on these results and others reviewed in his chapter, [Postle](#) argues that the PFC is related to attention or control-related processes, rather than memory storage *per se* (see also [Lebedev et al., 2004](#)).

[Marklund and Nyberg](#) also strongly argue for a dynamic/functional view of WM over the traditional multi-store approach. They argue that, “temporary retention of information in WM is ‘simply’ accomplished by the prolonged, selective activation of already existing long-term memory representations reflecting or corresponding to the recently encountered and to-be-retained sensory input(s)”. Their work demonstrates that PFC activity is not unique to WM tasks but is also evident in studies of episodic memory. They review evidence to suggest that various LTM processes engage the same regions of PFC that have long been implicated in WM maintenance. They therefore agree with [Postle](#) and claim that the PFC is related to attention or control processes rather than memory storage.

In sum, the chapters by [Postle](#), and [Marklund and Nyberg](#) present a strong challenge to researchers still holding to the multi-store approach made so popular by [Baddeley and Hitch](#). It seems that the conventional wisdom in the field, particularly from those with more of a neuroscience perspective, is that WM represents an emergent property of the mind and is achieved via both domain-general processes accomplished by PFC and related areas, as well as domain-specific processes accomplished by more posterior regions that are also associated with perception. By these views, the phonological loop (or any other ostensible storage structure) only “exists” as the simultaneous activity of frontal and posterior brain regions, each of which have primary functions quite independent of the short-term retention of information.

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## 2. The focus of attention in WM

An interesting new development in the area of WM has been an examination of the “focus of attention” in WM ([Garavan, 1998](#); [McElree, 1998](#); 2001; [Oberauer, 2002](#); [Verhaegen et al., 2004](#)). These studies have been largely motivated by [Cowan's](#) WM model (1988, 1995). As mentioned earlier, [Cowan](#) adopted the view that WM can be thought of as the active portion of

<sup>2</sup> This idea was actually first introduced by [Hebb \(1949\)](#) but [Anderson](#) incorporated it into a larger model of cognition.

long-term memory. He further argued that within this active portion of memory there is a *focus of attention* that retains a very limited number of items ( $4 \pm 1$ , Cowan, 2001). Items in the focus of attention enjoy a privileged status and are therefore immediately available for further processing. Items outside the focus must be retrieved. Thus, his model supposes three levels of representation: passive LTM, WM (i.e., active LTM), and focal attention.

Cowan's model inspired a number of experiments on the dynamics of attentional focus, such as how information occupies, retains, and loses focus. Several of these papers have examined "focus switching", the process of updating the contents of the focus of attention. For example, using the *n*-back task, McElree (2001) argued for a modification of Cowan's model. Using a response-deadline, speed-accuracy trade-off procedure, he demonstrated that there is privileged access to the most recent item in the *n*-back stream (as evidenced by greater accuracy at very brief response deadlines). McElree therefore claimed that the focus of attention is limited to just one item (cf. Garavan, 1998; Oberauer, 2002). He further argued that the retrieval dynamics governing retrieval from outside the focus of attention are the same as those that govern retrieval from LTM. According to this perspective there are only two levels of memory representation: inside the focus or outside the focus.

Two chapters in the Osaka et al. volume address this debate (Oberauer, Chapter 20; and Verhaegen et al., Chapter 5). Oberauer's approach accommodates both Cowan's argument for limited access to  $4 \pm 1$  items and McElree's argument for privileged access to just one item. He argues that information in WM is represented at one of three hierarchical levels; the activated portion of LTM, the region of direct access, and the focus of attention (to make things somewhat confusing, Oberauer's *region of direct access* corresponds to Cowan's *focus of attention*). Based on a series of empirical papers, Oberauer presents data to suggest that the focus of attention is limited to just one item, consistent with McElree (2001), and that the region of direct access is limited to  $4 \pm 1$  items, consistent with Cowan (2001). He further argues that there are several constraints that explain why WM is capacity-limited. One is that the number of independent bindings that can be maintained in the region of direct access is limited. Another is that elements in the region of direct access compete for the focus of attention. And yet another is retrieval competition from items outside the region of direct access, as evidenced by the multitude of data demonstrating interference effects in retrieval from LTM (for a similar view of capacity limits on WM, see Unsworth and Engle, 2007).

Verhaegen and colleagues take a different approach to focus switching. They challenge the notion that these states of representation, either two or three, represent fixed limitations on the WM system. Influenced by the idea of attention as a resource (Kahneman, 1973), they propose that attention can be flexibly allocated depending upon task demands and the participant's goals. Thus, attention can be narrowly focused on just one item, or expanded to accommodate up to four items (for a similar view, see Cowan, 2005).

They provide empirical support for this view via a working memory training experiment. Participants performed an *n*-back task for 10 h over 5 consecutive days. The logic of the

study was as follows: if privileged access to the most recent item in the *n*-back task is due to a hard structural limitation, then evidence for this privileged access should remain after extended practice. If, however, evidence for privileged access diminishes over practice, then a resource allocation view would be preferred. Indeed, after 10 h of *n*-back practice, participants demonstrated extremely fast reaction times (RT) for the most recent four items in the stream, not just the one most recent. Interestingly, there was still a distinction between RT to the fourth item and the fifth item. Verhaegen et al. therefore agree with Cowan, who argued that the hard limit is around  $4 \pm 1$  items.

In sum, several very clever experiments have investigated the dynamics of focal attention. These experiments are fundamental to the field of WM because they call into question the very notion of a limited capacity store (e.g., McElree, 2001). As well, they have the potential to differentiate mechanistic views of capacity limits (e.g., Oberauer, Chapter 20) from resource-based views (e.g., Verhaegen et al., Chapter 5).

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### 3. Variation in WM

Working memory is a limited capacity system, i.e., there is a limit to the number of distinct memory representations that can be maintained in a readily accessible state. Miller (1956) famously estimated the capacity of immediate memory to be  $7 \pm 2$  items. More recently, Cowan (2001) showed that when grouping strategies such as chunking are successfully prohibited from influencing task performance, the capacity is closer to  $4 \pm 1$ . More recent research has also demonstrated that there are striking individual differences in WM capacity: developmental differences in childhood and old age, differences due to mental disorders and disease, and even differences among healthy adults. What's more, these differences matter a great deal, as WM plays a critical role in a variety of complex cognitive behaviours, such as reasoning, language comprehension, and problem solving. While it is clear that there's a limit to WM, and variation in WM capacity is important, the source of variation in WM remains unclear. That is, the mechanisms that contribute to variation in WM are not fully understood. There have been many candidate mechanisms, such as a limit to the number of distinct bindings that can be actively maintained, interference control (e.g., inhibition of irrelevant information), information-processing speed, and motivation. Indeed, this is an active area of research, recently summarized in an edited volume on WM variation (Conway et al., 2007).

Several of the chapters in the Osaka et al. volume are devoted to variation in WM. Daneman and Hannon (Chapter 2), Cowan et al. (Chapter 3), and Osaka et al. (Chapter 6) all address individual differences among healthy adults. Neath and Suprenant (Chapter 10) and Rypma (Chapter 17) explore the effects of aging on WM. Finally, Martin and Hamilton (Chapter 11) review the neuropsychological approach to WM.

It is fitting that Daneman and Hannon take precedence in the volume at Chapter 2 because Daneman and Carpenter (1980) largely motivated the vast literature on individual differences in WM that has developed over the last 30 years. They demonstrated that, among healthy young adults, WM

span tasks predict reading comprehension better than traditional simple span tasks, such as digit span. WM span tasks require the maintenance of information in the face of concurrent processing. For example, the reading span task requires the participant to remember words for later recall while continually reading sentences. A variety of WM span tasks have now been developed; each consists of a storage component (e.g., remember words) and a processing component (e.g., reading sentences) and are therefore sometimes referred to as *storage-and-processing* tasks. Several studies have replicated Daneman and Carpenter's (1980) original result; WM span tasks predict higher-order cognition better than simple span tasks (Conway et al., 2002; Daneman and Merikle, 1996; Engle et al., 1999; Kane et al., 2004; but see Colom et al., 2006; Unsworth and Engle, 2006). The contentious issue that remains is *why* WM span tasks have broader predictive validity than simple span tasks. This issue is addressed by Daneman and Hannon (Chapter 2) and Cowan et al. (Chapter 3).

Daneman and Hannon (Chapter 2) focus on the relationship between WM span and reading comprehension. Their work demonstrates that WM span is differentially related to component processes underlying comprehension. For example, WM span is important for inferring and integrating text but is not important when understanding is accomplished by simply accessing prior knowledge in long-term memory. These results are important because they suggest that the mechanisms underlying the relationship between WM span and reading comprehension are domain-general rather than domain-specific (cf. Shah and Miyake, 1996; Kane et al., 2004), and they show that WM capacity is not associated with all cognition, broadly defined, as would be predicted by a motivation account.

Cowan et al. (Chapter 3) also provide evidence to suggest that the relationship between WM span and complex cognition is largely domain-general. They go beyond this to explore the precise mechanisms involved in WM span and more complex tasks, like reading and reasoning. Cowan et al. argue that the capacity of the focus of attention and the control of attention are separable constructs and that each contributes to variation in cognitive performance. The capacity of attention refers to the limited number of representations that can simultaneously occupy the focus of attention while the control of attention refers to cognitive control mechanisms such as selection and inhibition. Cowan's recent work shows consistent individual differences on tasks designed to assess the capacity of attention, tasks designed to assess the control of attention, and intelligence. Moreover, there is a high degree of overlap in capacity and control measures, yet each account for some unique variance in intelligence as well.

Osaka and Osaka (Chapter 6) explore individual differences in WM in healthy adults using fMRI data. They review recent studies in which participants with high- and low-WM capacity perform WM span tasks, under fMRI. In their own study, Osaka, Osaka, and colleagues administer a WM span task, e.g., reading span, as well as the storage component alone, e.g., remember words, and the processing component alone, e.g., read sentences. Neural activity associated with the WM span task is compared to storage-only and then to processing-only and then the conjunction of these two

analyses is taken as evidence of activity associated with WM span, above and beyond the component parts (for similar studies, see Bunge et al., 2001; Smith et al., 2001). Each of these studies has shown that WM span performance is linked to activity in the dorsolateral PFC (DLPFC), anterior cingulate cortex (ACC), and sometimes posterior parietal areas.

In terms of individual differences, Osaka, Osaka, and colleagues have shown that high-WM span individuals show greater signal intensity in ACC during the WM span task than individuals with lesser WM. Also, high-WM individuals show greater functional connectivity (i.e., a higher degree of correlation in signal change) between DLPFC and ACC during the WM span task. The ACC has previously been shown to be involved in conflict monitoring (Botvinick et al., 2001), e.g. situations in which a task goal conflicts with a habitual or prepotent response, such as in the Stroop task. Individual differences in ACC activity associated with WM span are therefore quite interesting because previous behavioural work comparing high- and low-WM span individuals has shown that high-WM individuals are better at maintaining task goals, particularly in the face of conflict (e.g., Kane and Engle, 2003). Thus, Osaka, Osaka, et al.'s chapter presents a valuable synthesis of neuroimaging and individual differences approaches to WM.

Rypma (Chapter 17) reviews his recent fMRI work exploring the effects of age on WM. A great deal of prior behavioural work has shown that WM performance declines with age. WM decrements with age are thought to reflect slower information-processing speed (e.g., Salthouse, 1996) as well as deficiencies in cognitive control mechanisms, such as inhibition (e.g., Hasher and Zacks, 1988). With respect to imaging studies, older adults often show *increased* neural activity during WM performance relative to younger adults. This is somewhat counterintuitive given Osaka et al.'s results showing increased activity in high-WM relative to low-WM individuals. To account for this paradox, Rypma advances the neural efficiency hypothesis of age-related changes in WM. According to his theory, increases in activation associated with age are related to decrements in the efficiency of transmission mechanisms that are responsible for a particular cognitive process. Rypma reviews a series of studies that support this efficiency view over a compensatory theory, according to which older adults compensate by adopting more elaborate strategies to perform cognitive tasks.

Neath and Suprenant (Chapter 10) explore age-related changes in WM performance with an emphasis on the phonological loop, which was originally proposed to account for several basic memory phenomena, such as the word length effect and the irrelevant speech effect. As noted by Neath and Suprenant, given the importance of these basic phenomena to memory theory, it is somewhat surprising that so little attention has been paid to the effects of age on these basic effects. Neath and Suprenant attempt to address this gap in the literature by modelling age-related change in the word length effect, the irrelevant speech effect, the concurrent articulation effect (aka articulatory suppression), and the acoustic confusion effect (aka the phonological similarity effect) using Nairne's (1990) feature model of memory, which can account for most, if not all, immediate serial recall phenomena. Their results show that the feature model can handle age-related changes in these effects but they admit that

this is a relatively under-studied area and call for more research along these lines. We agree and would add that more work is needed when it comes to computational modelling accounts of variation in WM.

Another area of research that, in our opinion, deserves more attention in the WM literature is cognitive neuropsychology. Martin and Hamilton (Chapter 11) provide an excellent overview of research with brain-damaged patients that has implications for WM theory. In particular, they present patterns of behaviour in an individual patient (ML) across a range of tasks that are inconsistent with correlational data across the same set of tasks in healthy participants. For example, in samples of healthy participants, individuals with greater WM tend to perform above average on a range of tasks that tap cognitive control, such as the Stroop task and the antisaccade task, which requires the participant to make an eye-movement in the opposite direction of a flashing stimulus. In contrast, patient ML demonstrates a deficit in short-term memory and Stroop performance but is not impaired on the antisaccade task. To account for these paradoxical effects, Martin and Hamilton suggest that perhaps individual differences in healthy adults are due to differences in the function of neurotransmitters, such as dopamine, whereas patient deficits are due to structural abnormalities as a result of stroke, disease, or injury. This is an interesting account and more work along these lines is needed, to compare and contrast individual differences in healthy adults, developmental differences in childhood and old age, and deficits due to injury or disease.

#### 4. Computational models of WM

A critical question facing all theoretical accounts of working memory is how a system that is responsible for maintaining information, particularly in the face of interference, nevertheless flexibly updates that information in a timely and goal-directed manner. In our opinion, the most striking contemporary advances toward providing an answer to this question have come from computational modelling. Unfortunately, these approaches were not included in the Osaka et al. volume. In keeping with our coverage of broad themes in the WM literature, we describe what we think are the most exciting developments in this area.

All biologically plausible models of WM function emphasise the interaction of PFC activation with representations in other parts of the cortex. Recurrent activation, in which a set of neurons activate another set that, in turn, reactivates the first set, can give rise to attractor states – emergent, stable patterns of activation that represent information (Hopfield, 1982). This approach allows a system to exhibit delayed maintenance of representations. Some models have included interactions between cortical and subcortical structures as the explicit mechanism by which recurrent activation is generated (Ashby et al., 2005; Monchi et al., 2000; Taylor and Taylor, 2000). However, models that rely on this kind of continuous reverberating activation to represent information suffer from a common problem: they can maintain information but not flexibly update it in a realistic fashion (Braver and Cohen, 2000). Several recent models leverage interactions

between subcortical structures and PFC in order to address the question of representation-updating.

One solution to the updating problem is to instantiate a ‘gating’ mechanism that can toggle updating of representations (Hochreiter and Schmidhuber, 1997). This mechanism functions essentially as a switch: when it is on, incoming information can update WM representations; when it is off, no updating is allowed, and current representations are maintained in a robust fashion. Using this strategy, Braver and Cohen, 2000 articulated a model of prefrontal and subcortical interaction in a WM task, the AX-CPT. This delayed performance task requires participants to maintain context information about a recent cue while engaged in the search for a target amidst continuously presented distractors and to rapidly update cue representations over time (i.e., respond to an X if, and only if, it’s preceded by an A). Their model accomplishes two very important feats not previously addressed by other WM models: it successfully explains how a gating mechanism, instantiated by the ventral tegmental area (a subcortical brainstem structure), might enable updating of maintained representations and it demonstrates how a system can ‘learn’ to update appropriately using non-controversial learning principles (connected to dopaminergic functioning; Braver and Cohen, 2000; Montague et al., 1996; Sutton and Barto, 1998). This model, however, does not address the issue of selective updating: how does WM update some representations without updating all current representations (Braver and Cohen, 2000)?

Frank et al. (2001) proposed a model of PFC-basal ganglia interaction that addresses this issue by separating the gating and learning mechanisms while extending the scope of the biological detail on which the model is based (see also Hazy et al., 2007; O’Reilly and Frank, 2006). This model, termed PBWM (PFC, Basal ganglia, WM model), performs a modified version of the AX-CPT, called the 1-2 AX-CPT, in which simultaneous maintenance of current context information and rapid updating of incoming stimulus contingencies are required (O’Reilly and Frank, 2006). In brief, if a 1 is seen, the target sequence is AX; if a 2 is seen, it is BY. Thus, some WM representations need to be rapidly updated (was the last stimulus an A or a B?) while others need to be concurrently maintained (was there a 1 or 2 last?). Successful performance is based on multiple parallel circuits between PFC and basal ganglia. Sensory input causes transient signals in PFC, but experience, in the form of reinforcement learning, dictates which signals will trigger the gating function and which will not. Those stimuli previously reinforced can trigger inhibition of substantia nigra pars reticulata (SN) neurons via connections through dorsal striatum. This prevents the normal, chronic inhibition of thalamic nuclei by the SN. With the thalamus disinhibited, additional excitation passes into PFC. This additional activation is the gating function, triggering PFC neurons to change their firing patterns, thus biasing subsequent stimulus processing (O’Reilly and Frank, 2006).

The critical difference between this model (see also Braver and Cohen, 2000) and those depending on continuous recurrent excitation (e.g., Ashby et al., 2005) is that here, activity between PFC and thalamus is transient. Activation of the thalamic units in this model not only triggers updating of select WM contents, but also triggers an automatic cessation of updating activity. This occurs because an indirect pathway

exists from thalamus to SN (mediated by complex circuits involving globus pallidus, dorsal striatum, and the subthalamic nucleus) that reinitializes the tonic inhibition of the thalamus (Hazy et al., 2007). Thus, the gate closes itself by default. The interaction of this mechanism with PFC neurons that can maintain firing on their own (cf. Wang, 1999) gives rise to flexible, goal-directed behaviour on a WM task. Experience with success and failure in a task trains the PFC-caudate network to update only relevant stimuli (e.g., 1, 2, A, or B). Thus, gating will occur when appropriate in the context of past experience, and the current contents of WM will be maintained by PFC neurons on their own until another salient stimulus triggers updating of these representations. These representations can be updated independently of one another (e.g., update the most recent A or B without updating 1 or 2) as a consequence of multiple, parallel circuits between PFC and basal ganglia structures (Frank et al., 2001).

These models represent a brief selection of the most recent advances in neurobiologically plausible computational models of WM. The need for a homuncular central executive is eliminated by a mechanistically explicit gating function and the use of reinforcement learning algorithms to train the gating function. The interaction of these systems with multiple parallel PFC-basal ganglia circuits gives rise to the emergence of goal-directed WM performance. Understanding these models is critical to the developing cognitive neuroscience of WM. They have provided the first mechanistic account of a key aspect of WM function: goal-directed and selective updating of maintained representations. In so doing, they explicitly conceive of WM as an emergent result of interactions between control representations in PFC and representations in other areas of cortex. This clearly supports dynamic attentional control theories of WM function, as opposed to structural store models or computer metaphors. These models also provide a framework within which to interpret emerging neuroimaging and behavioural results, including clinical data (e.g., Braver et al., 1999; Frank et al., 2004).

## 5. Conclusion

In sum, Osaka, Logie, and D'Esposito have done an outstanding job of bringing together a series of interesting chapters on the topic of WM. The book captures a number of important themes that are currently running through contemporary research on WM. This volume should be required reading for anyone interested in the current state of the field. We would also argue that it's important to track the recent developments in the field of computational modelling, as discussed above. Taken together, the reader will enjoy a comprehensive review of the cognitive neuroscience of WM.

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