Using neuroimaging to evaluate models of working memory and their implications for language processing

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Abstract

The precise relationships that exist between verbal working memory and language processing remain underdetermined. We argue that while neuroimaging methods have the potential to provide important insights into the links between these two cognitive domains, an over-reliance on a single theoretical perspective has stunted progress toward this end. Specifically, neuroimaging studies in the domain of working memory have relied heavily on the theoretical framework provided by Baddeley's Multiple-Component Model. We reexamine the sufficiency of this model in accounting for a range of neuroimaging evidence, and draw attention to a set of findings that are not readily explained by a conventional mapping of this model onto specific neuroanatomical substrates. An alternative framework provided by Cowan's Embedded-Processes Model is then evaluated, and we conclude that this alternative view supports a reconceptualization of the contributions of Broca's area and the left inferior parietal cortex to working memory that can account for a wide range of findings. Importantly, this alternative account suggests links between working memory and language that are not afforded by currently prevailing interpretations.
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For the past 15 years, functional neuroimaging studies have played an important role in identifying brain structures associated with various cognitive tasks (Cabeza & Nyberg, 2000; Posner, Abdullaev, McCandliss, & Sereno, 1999). However, a shortcoming of

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neuroimaging research is that it has too often failed to make contact with theoretical models of cognition (for relevant arguments see e.g. Poeppel, 1996; Raichle, 1998). The domain of working memory may appear to be an exception to this generality, because many neuroimaging findings in this area have been specifically interpreted in the context of a widely adopted cognitive model (Baddeley's Multiple-Component Model). Although these efforts have yielded a mapping between neural substrates and proposed cognitive processes, they have also largely ignored competing models of working memory.

There are several well-articulated models of working memory (Miyake & Shah, 1999; Richardson, Engle, Hasher, & Logie, 1996); these models differ in fundamental ways, but each generally succeeds in accounting for the available behavioral evidence. Thus, behavioral findings alone have proven to be insufficient (so far) as a means of adjudicating between alternative theories. Neuroimaging methods, however, have the potential not only to localize the neural substrates of working memory, but more importantly, to provide a novel set of constraints that may help in evaluating the adequacy of alternative models. In so doing, neuroimaging can play a critical role in motivating important theoretical advances. Furthermore, although models of working memory often make little contact with models of language processing, we will argue below that neuroimaging data can be used to highlight and understand important points of connection that have been generally overlooked (for related discussion see Smith & Geva, 2000).

We will begin by briefly describing the neuroanatomical substrates of verbal working memory, and will then turn to an evaluation of the fit between neuroimaging data and two successful models of working memory: the Multiple-Component Model proposed by Baddeley and colleagues (Baddeley & Logie, 1999), and the Embedded-Processes Model proposed by Cowan and colleagues (Cowan, 1999). We conclude that the Embedded-Processes Model readily accounts for a range of findings that are difficult to explain within the framework of the Multiple-Component Model. Importantly, the Embedded-Processes Model succeeds in part by providing an account of the connections between working memory, speech-based rehearsal, and the encoding of phonological features that consequently generates new hypotheses about the relationship between the component processes of working memory and the component processes of language tasks, such as reading and sentence comprehension.

1. Neuroimaging and the functional anatomy of working memory

To date, there are nearly a hundred neuroimaging studies that have investigated brain activity during performance of a working memory task using verbal stimuli (e.g. letters, words, digits), and many others that have investigated working memory with non-verbal stimuli (e.g. spatial locations, abstract objects, faces). Reviews of this literature (Cabeza & Nyberg, 2000; D'Esposito, Aguirre, Zarahn, Ballard, Shin, & Lease, 1998; Fiez et al., 1996; Owen, 1997) suggest that a remarkably consistent network of neuroanatomical regions is implicated across studies.

The major constituents of the verbal working memory network observed through neuroimaging are shown in Fig. 1 (note that several of these regions also support non-verbal maintenance). Within the lateral prefrontal cortex at least three distinct sites are
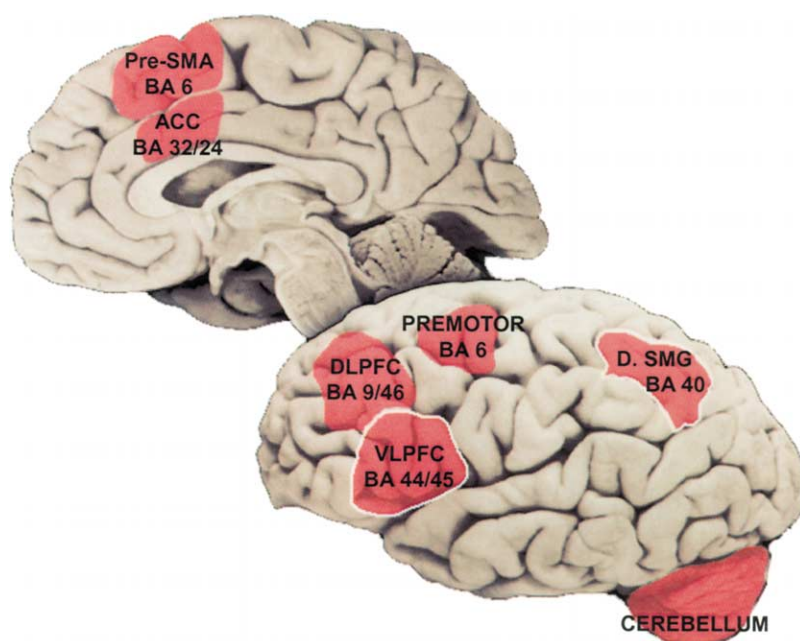
Fig. 1. The network of regions consistently implicated in neuroimaging studies of verbal working memory. This network is comprised of the dorsolateral prefrontal cortex (DLPFC), the ventrolateral prefrontal cortex (VLPFC), the premotor cortex, the pre-supplementary motor area (pre-SMA), the anterior cingulate cortex (ACC), and the cerebellum. Functions of the regions bordered in white are discussed most heavily in the present paper. Image modified from Sylvius: Fundamentals of Human Neural Structure, S. Mark Williams, Sinauer Associates, inc. Sunderland MA.

implicated, one in a dorsolateral region encompassing Brodmann's areas (BA) 9 and 46 of the middle frontal gyrus (often bilateral), one located more ventrally in the inferior frontal gyrus (BA 44,45; Broca's area and sometimes its right hemisphere homologue), and one in the premotor cortex (BA 6, often bilateral). Activation of the pre-supplementary motor area (pre-SMA, BA 6), located in the medial frontal cortex, is also consistent, and this activation often encompasses a portion of the anterior cingulate cortex (found immediately ventral to the pre-SMA). In the parietal cortex, activation of the dorsal aspect of the supramarginal gyrus (BA 40, bilateral) in the left inferior parietal lobule is most reliable. Finally, lateral cerebellar areas are also implicated in numerous studies of verbal working memory.

While for the purposes of this paper we will treat each of the aforementioned regions as functionally homogeneous, we note that there is a growing body of literature suggesting that each may be comprised of multiple subregions that make dissociable contributions to working memory. We have previously observed, for example, that the neuropsychological and neuroimaging literatures appear to emphasize two anatomically, and possibly functionally, distinct subregions of the inferior parietal cortex (Becker, MacAndrew, & Fiez, 1999; Fiez, 2001; Ravizza, Delgado, Chein, Becker, & Fiez, submitted for publication). Similarly, we have reported both empirical and meta-analytic evidence of

functional heterogeneity between two subregions of Broca's area (Chein & Fiez, 2001; Chein, Fissell, Jacobs, & Fiez, 2002).

2. Baddeley's multiple-component model

Baddeley and colleagues (Baddeley, 1995, 1986; Baddeley & Hitch, 1974) articulated a model of working memory that made two important breaks with traditional views in memory research. First, they claimed that short-term, or working, memory was an independent system that should be distinguished from long-term memory, and second, that it should be viewed as an active process (rather than a passive repository) dedicated specifically to the temporary maintenance and manipulation of task-relevant information. The model successfully accounts for a large set of behavioral findings in an intuitive manner. It is thus not surprising that it has become the predominant model of working memory in cognitive psychological and neuropsychological research, as evidenced in part by the citation frequency of the original work (Baddeley & Hitch, 1974, has been cited over 2000 times). Neuroimaging investigators have followed suit, and have relied almost exclusively upon the Multiple-Component Model to understand the specific contributions of brain regions that are active during verbal working memory tasks (Henson, 2001; Smith & Jonides, 1997).

The structure of the Multiple-Component Model is depicted in Fig. 2(A). The model asserts that there are separate systems responsible for the maintenance of distinct types of information; a subsystem specialized for maintaining verbal (linguistic, speech-like) material, referred to as the *phonological loop*, and a subsystem specialized for maintaining non-verbal (spatial, form-based) material, referred to as the *visuospatial sketchpad*. Baddeley's model also posits a separate attentional controller, the central executive, which guides the behavior of the maintenance subsystems, provides them with additional processing capacity, and supports the monitoring and manipulation of the information in working memory.

The verbal maintenance subsystem of the Multiple-Component Model (i.e. the phonological loop) is further divided into two subcomponents, a passive *phonological store* that retains verbal information through phonological representations (that are subject to decay), and an active *rehearsal process* that refreshes these representations in a manner equated with subvocalization or 'inner speech'. It is important to recognize that current versions of the model (Baddeley & Logie, 1999) assume that the rehearsal process is not itself a dedicated storage device, but serves specifically to support maintenance in the phonological store. Rehearsal is thus assumed to be an optional, though often strategic, way to retain information over durations that exceed the temporal decay limits of the store. The subvocalization process used for rehearsal is also thought to allow recoding of visually presented verbal information into a form suitable for storage, whereas auditory-verbal information is assumed to have obligatory and direct access to the phonological store.

Evidence for the phonological storage and rehearsal processes of Baddeley's model derives in part from behavioral phenomena in working memory performance. The *phonological similarity effect* and the *irrelevant speech effect* are two phenomena thought to be linked to the operation of the phonological store. The *phonological similarity effect*
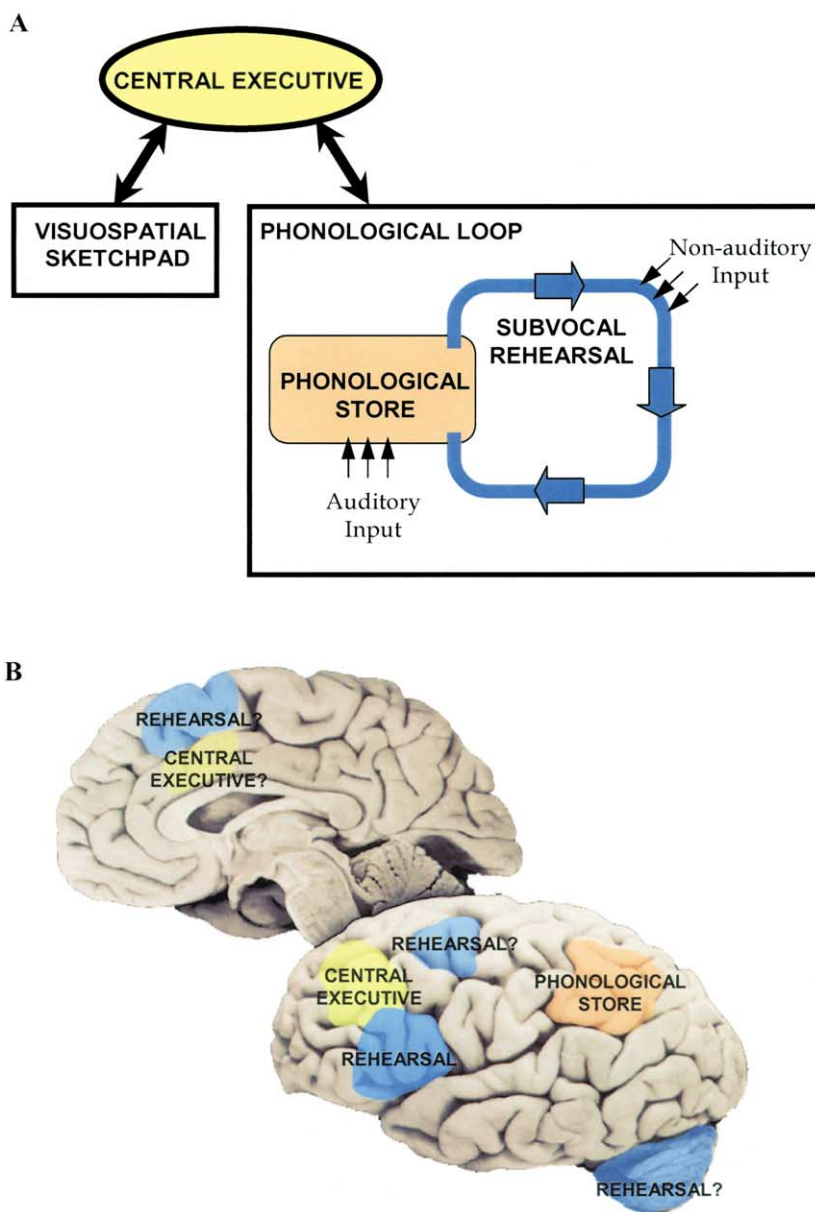
THE MULTIPLE-COMPONENT MODEL

Fig. 2. The Multiple-Component Model (Baddeley, 1986). Panel A illustrates the main structural and processing components of the Multiple-Component Model, adapted from (Baddeley, 1986). Panel B illustrates a tentative, but fairly widely accepted, mapping of the Multiple-Component Model onto the brain. Regions are color coded to correspond to the model components shown in panel A. Images modified from Sylvius Fundamentals of Human Neural Structure, S. Mark Williams, Sinauer Associates, inc. Sunderland MA.

refers to the advantage in immediate serial recall for items that sound distinct (e.g. pig, bun, car), as compared to items that sound alike (e.g. mat, mad, map) (Conrad, Freeman, & Hull, 1965), and is assumed to arise from interference among items in the store having a similar phonological code. The *irrelevant speech effect* refers to the deleterious effect of having extraneous speech sounds in the background as a subject attempts to perform a working memory task (Colle & Welsh, 1976; Salame & Baddeley, 1982), and is thought to arise from the interference that these auditory background sounds cause upon obligatory entry into the store.

The *word length effect* and the effect of *concurrent articulation* are two behavioral markers of the speech-based rehearsal process. The word length effect refers to the relative advantage in immediate serial recall for items that have shorter (e.g. pig, bun, car), as compared to longer (e.g. kangaroo, computer, telescope), spoken durations (Baddeley, Thomson, & Buchanan, 1975). *Concurrent articulation* refers to the dramatic reduction in working memory task performance when subjects are required to overtly or covertly repeat an irrelevant speech token (e.g. 'the, the, the, …') during each working memory trial (Murray, 1968). Both of these effects are taken as evidence of a link between general speech planning mechanisms and the speech-based rehearsal process used to support maintenance.

Importantly, the separability of storage and rehearsal components in verbal maintenance is also indicated behaviorally. Evidence for this dissociation comes from the observation that concurrent articulation removes the word-length effect, but not the phonological similarity effect, when items are presented auditorily (Baddeley, Lewis, & Vallar, 1984; Longoni, Richardson, & Aiello, 1993). Baddeley and colleagues interpret this finding by assuming that concurrent articulation ties up the speech planning resources necessary for the rehearsal process, hence eliminating the advantage of short words over long words. Meanwhile, concurrent articulation does not have an impact on the operation of the phonological store itself; thus, the advantage in recalling lists of phonologically distinct items persists when they can gain direct access to the store through auditory presentation.

Studies of neurologically impaired patients provide further evidence of separate storage and rehearsal components, and offer preliminary indications of their neuroanatomical localization. In particular, it has been observed that patients with posterior lesions (especially including the left ventral supramarginal gyrus) exhibit very limited auditory-verbal spans (Cappa & Vallar, 1988; Shallice & Vallar, 1990; Vallar & Cappa, 1987). Meanwhile, patients with anterior lesions (near Broca's area) exhibit detectable, but less significant, span impairments, despite obvious difficulties with overt articulation (Martin, 1987; Vallar, Corno, & Basso, 1992; Wise, Greene, Buchel, & Scott, 1999). Shallice and Vallar (1990) have argued that this pattern of results can be interpreted by assuming that posterior lesions impair the operation of the phonological store, while lesions in frontal areas (which are often implicated in speech, Fuster, 1995; Mohr, 1976) impair the rehearsal process.

3. Mapping Baddeley's multiple-component model onto neuroimaging data

Numerous features of Baddeley's framework have been addressed directly in neuroimaging studies. These include the distinction between verbal and visuo-spatial

maintenance subsystems (Smith, Jonides, & Koeppe, 1996), the dissociability of storage and rehearsal in verbal maintenance (Awh et al., 1996; Paulesu, Frith, & Frackowiak, 1993), and the distinction of a central executive processor from the subsidiary maintenance subsystems (Collette & Van der Linden, 2002; D'Esposito, Detre, Alsop, & Shin, 1995; Salmon, Van der Linden, Collette, & Delfiore 1996). It is generally agreed that each of these features is corroborated by the neuroimaging findings (Hartley & Speer, 2000; Henson, 2001; Jonides, 2000; Smith & Jonides, 1997, 1998, 1999).

Moreover, a specific mapping between components of the multiple-component model and particular regions of the brain has been proposed (Henson, 2001; Smith & Jonides, 1999). As shown in Fig. 2(B), this mapping places the phonological storage component of the verbal maintenance subsystem into the left supramarginal gyrus (BA 40). Meanwhile, the speech-based rehearsal process is attributed principally to Broca's area (BA 44/45), with possible additional contributions from premotor, pre-SMA, and cerebellar areas. Finally, executive control is thought to arise largely through the operation of the dorsolateral prefrontal cortex (BA 9/46). Given our ultimate objective of exploring links between working memory and language, we limit discussion of the empirical bases for this mapping to evidence regarding the presumed substrates of the verbal maintenance subsystem (i.e. phonological storage and speech-based rehearsal in the phonological loop).

Early neuroimaging evidence consistent with Baddeley's distinction of a phonological storage component and a separate speech-based rehearsal process was provided by Paulesu et al. (1993). This study included a verbal working memory task condition (delayed item recognition with English letters), a non-verbal working memory condition (delayed recognition of Korean letters), and a rhyme judgment task condition. A verbally specific working memory network, including inferior frontal, supplementary motor, inferior parietal, and cerebellar areas was first identified by contrasting the verbal working memory condition with the non-verbal working memory condition. Since it had been argued in prior research that rhyme judgments engage the rehearsal process (Besner, 1987; Burani, Vallar, & Bottini, 1991; Vallar & Baddeley, 1984), Paulesu et al. further assumed that the speech-based rehearsal system could be removed, and the phonological store revealed, by subtracting activity in the rhyme judgment condition from that in the verbal working memory condition. This subtraction eliminated previously significant activations in several relevant regions (e.g., Broca's area, cerebellum, SMA) and yielded significant activity only in the left inferior parietal cortex (ventral supramarginal gyrus), the brain region previously implicated in storage through neuropsychological research (Shallice & Vallar, 1990).

Awh et al. (1996) sought to provide further evidence of separate phonological storage and speech-based rehearsal processes using a similar strategy. The entire verbal working memory network was first identified by contrasting a verbal working memory task with a sensorimotor control condition. This contrast identified activity specific to working memory in several cortical regions, including Broca's area, left premotor cortex, the pre-SMA, the right cerebellum, the anterior cingulate, and the left inferior parietal cortex. To identify regions contributing separately to rehearsal and storage, Awh et al. (1996) included an additional 'rehearsal' control condition, in which subjects viewed sequentially presented items and were instructed to continuously and covertly repeat each item until

the subsequent item arrived. Subtracting activity in this silent repetition condition from that in the working memory condition was again expected to remove much of the rehearsal system, but not the phonological store. Seemingly consistent results were obtained, with left anterior 'speech' regions (Broca's area and left premotor cortex) subtracted out, but the left supramarginal gyrus (among other regions) still activated differentially.

On the surface, such investigations in the domain of verbal working memory reflect a rare success in establishing close links between neuroimaging results and cognitive theory. However, we argue below that the focus on a single theory of working memory has led researchers to overlook alternative theoretical accounts that may actually prove more accommodating of the data. To develop this argument, we focus on the presumed contributions of the inferior parietal cortex to phonological storage, and of Broca's area to speech-based rehearsal. We highlight how these mappings are inconsistent with several lines of evidence, and we then examine how an alternative framework, the Embedded-Processes Model, can account for the observed data.

4. Re-evaluating the role of parietal cortex in phonological storage

The results from Awh et al. (1996) and Paulesu et al. (1993) serve as the primary neuroimaging evidence for a storage-rehearsal distinction in the brain. However, it is important to recognize that while both studies suggest that the parietal cortex is not instrumental in rehearsal, neither specifically shows that it makes a contribution to phonological storage. Based upon Baddeley's notions of phonological storage, at least four properties might be predicted of a region that serves as the store: (1) the region should be active specifically for verbal (phonologically codable) stimuli, and not for non-verbal stimuli, (2) activation of the region should persist across a delay interval, during which time the contents of the store are being repeatedly refreshed, (3) both passive listening and verbal working memory tasks should elicit activation in the region, since auditory verbal information has obligatory access to the store, and (4) the region's level of activation should be sensitive to phonological similarity, since this effect is considered a marker of phonological storage.

The left parietal cortex does not reliably demonstrate any of these properties. First, although this region is typically active in studies of verbal working memory, the same parietal region is also commonly implicated in studies using non-verbal stimuli (Belger et al., 1998; Carlson et al., 1998; Klingberg, 1998; Nystrom et al., 2000; Owen et al., 1998; Reuter Lorenz et al., 2000; Smith, Jonides, & Koeppe, 1996; Zurowski et al., 2002). Such findings suggest that parietal cortex is a material-independent processing region, and not a region contributing selectively to phonological representation. Second, several studies employing recall (as opposed to recognition) procedures have failed to identify significant delay-related activity in the left parietal cortex (Becker et al., 1994; Chein & Fiez, 2001; Fiez et al., 1996; Grasby et al., 1993; Jonides et al., 1998). Third, studies using non-mnemonic tasks involving auditory verbal stimuli (sentence comprehension, Friederici, Meyer, & von CDrammon, 2000; passive listening to words, Petersen, Fox, Posner, Mintun, & Raichle, 1988) report no significant parietal activation. Finally, activity in

the parietal cortex does not seem to be selectively affected by the phonological similarity of remembered items (Chein & Fiez, 2001).

5. Re-evaluating Broca's area and rehearsal

The assertion that Broca's area mediates rehearsal as concieved in Baddeley's model should also be viewed with some skepticism. Again, Baddeley's notions of speech-based rehearsal can be used to derive a set of expectations for a rehearsal-specific region: (1) the region should be active during simple speech tasks that are analogous to those used to produce a concurrent articulation effect, since this effect is presumably mediated by competing demands for the same processing resources, (2) the region should be active during tasks that are themselves disrupted by concurrent articulation, (3) the region should be sensitive to manipulations of articulatory length in a working memory task, since this has been viewed as a marker of speech-based rehearsal, and (4) the region should be less active during task conditions that discourage the use of a rehearsal strategy.

Patterns of activity in Broca's area are only partially consistent with these expectations. Tasks that are disrupted by concurrent articulation include verbal working memory, rhyme judgments, and complex sentence comprehension, all of which appear to produce activation in Broca's area. However, although Awh et al. (1996) found Broca's area to be activated in a silent-repetition task, several other studies employing covert speech tasks have reported contradictory results (Fiez et al., 1996; Gruber, 2001; Gruber & von Cramon, 2001). Interestingly, Gruber (2001) found that Broca's area was actually disengaged when subjects were required to carry out covert concurrent articulation (i.e. by silently repeating the numbers 1–4). Relatedly, two other studies (Caplan, Alpert, Waters, & Olivieri, 2000; Nystrom et al., 2000, exp. 3) have found that Broca's area remains sensitive to stimulus manipulations even under concurrent articulation. Moreover, we have shown (Chein & Fiez, 2001) that Broca's area is not selectively sensitive to word length manipulations. Finally, although Baddeley conceives of rehearsal as optional, Broca's area seems to be active under task conditions that should force subjects to abandon a rehearsal strategy. For instance, Coull, Frith, Frackowiak, and Grasby (1996) have found evidence of Broca's area activity even with rapid stimulus presentation, even though Coltheart (Coltheart, 1993; Coltheart & Langdon, 1998) has argued that rehearsal is precluded at rates that exceed the rate of inner speech (note that the maximal rate of presentation used by Coull et al. was 250 ms per item, while Coltheart and colleagues have used rates of 100–125 millisecond per item). Likewise, Broca's area is active when subjects are required to maintain the last several items in a list of arbitrary length (Postle, Berger, Goldstein, Curtis, & D'Esposito, 2001), even though this type of running memory span procedure is believed to discourage a rehearsal strategy (Cowan, 1995).

6. The embedded-processes model

We turn now to one alternative model, forwarded by Nelson Cowan (Cowan, 1988, 1993, 1995), which he has recently termed the Embedded-Processes Model (Cowan,

1999). Following the tradition of Broadbent (1958) and Norman (1969), the main intent of this model is to account for a wide range of empirical findings in the fields of attention and working memory within one common framework. Unlike Baddeley, Cowan contends that working memory entails the activation of representations in long-term memory, and not the engagement of a separate memory system (Anderson & Bower, 1973; Norman, 1968). Cowan further emphasizes that maintenance in working memory may be supported by rehearsal, but also by an alternative, material-independent, covert process. Therefore, though Cowan has at times likened his view to Baddeley's (Cowan, 1993), there are some fundamental distinctions, including: (1) working memory is viewed as a subset of long-term memory, rather than as a dedicated temporary storage system, (2) short-term memory for distinct types of stimuli (e.g. verbal, visuospatial) occurs within a common storage medium (long-term memory), and not in material-specific maintenance subsystems, and (3) strategic processes other than speech-based rehearsal are thought to play a significant role in reactivating stored information.

The basic structural elements of Cowan's model are shown in Fig. 3(A). In the Embedded-Processes Model, there is just one memory repository (though there is also a very brief sensory buffer). This single memory store is equated with the long-term memory system, and is presumed to hold representations as sets of associated features (or feature combinations). Importantly, information in this system can be made more readily accessible (i.e. brought into working memory) in one of two ways. First, an 'embedded' subset of information in the long-term store can be placed into a temporarily heightened state of activation. This activation is time-limited and subject to decay (Cowan, 1988; Hebb, 1949). Second, a further subset of this activated information can be made even more salient by bringing it into the *focus of attention*. The focus of attention is capacity-limited, and can 'shine' upon only a small amount of information at any one time. Working memory is assumed to comprise all information in a readily accessible state by virtue of its activation, including information within the focus of attention, as well as information in an activated state outside of attention (though a minimal activation threshold may apply, Cowan, 1995).

As in Baddeley's framework, the Embedded-Processes Model assumes a central executive component that provides a domain general processing capacity. Among other functions, this executive supervises covert processes that serve to maintain information over time (e.g. to reactivate decaying activity). While Cowan does not exclude speech-based rehearsal as one such reactivating mechanism, he emphasizes that searching through a set of memory items, by passing them through the focus of attention, can also serve this function (Cowan, 1992, 1999). Cowan and his colleagues have likened this reactivating search process to Sternberg's (1966, 1975) notion of fast memory scanning, and contend that there are several examples of its dissociability from speech-based rehearsal (Clifton & Tash, 1973; Cowan et al., 1998). We will hereafter refer to this alternative covert reactivation strategy as *attentional scanning*.

7. Mapping the embedded processes model onto neuroimaging data

Due in part to the predominance of Baddeley's model across disciplines, other models, including Cowan's, have received very little attention in neuroimaging research. However,
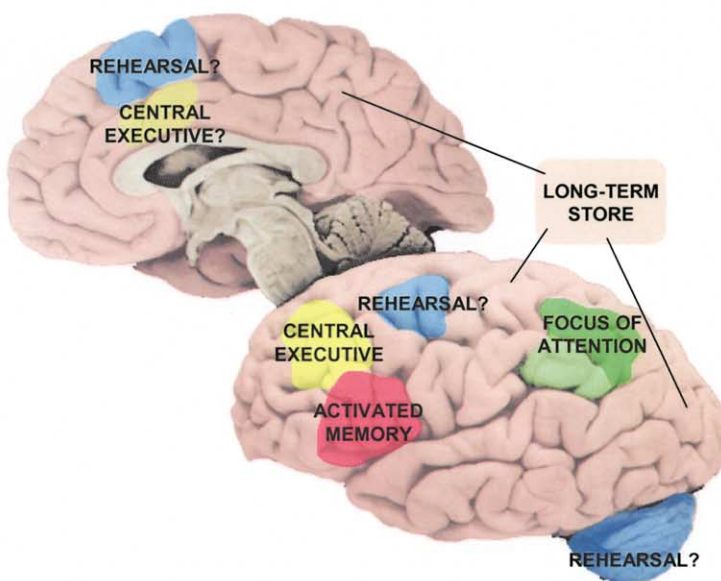
THE EMBEDDED-PROCESSES MODEL
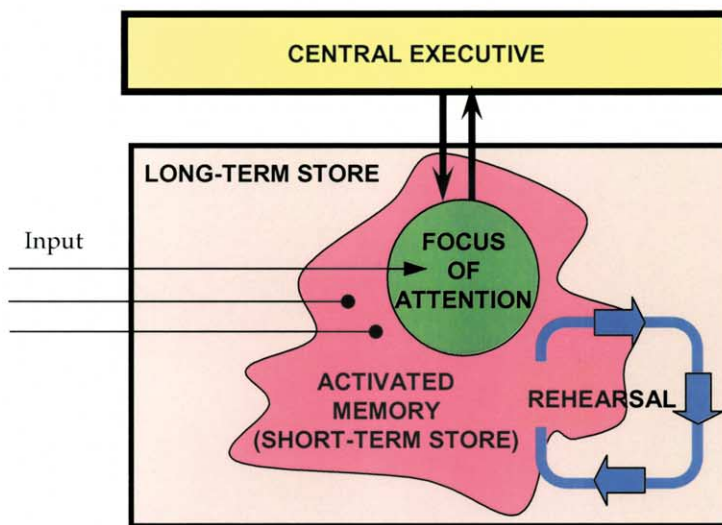
Fig. 3. The Embedded-Processes Model (Cowan, 1999). Panel A illustrates the main features of the Embedded-Processes Model, adapted from Cowan (1995). Panel B illustrates a tentative mapping of the Embedded-Processes Model onto the brain. Regions are color coded to correspond to the model components shown in panel A. Images modified from Sylvius: Fundamentals of Human Neural Structure, S. Mark Williams, Sinauer Associates, inc. Sunderland MA.

the Embedded-Processes Model maps fairly readily onto neuroanatomical data, and is thus amenable to evaluation through neuroimaging findings. Cowan himself (Cowan, 1995, 1999) has speculated on the mapping between the Embedded-Processes model and particular brain structures. A tentative mapping derived from Cowan's speculations is depicted in Fig. 3(B).

Under the framework of the Embedded-Processes Model, representations of existing knowledge are viewed as distributed throughout the neocortex. When external stimuli or internal processes activate a given memory representation, the particular activated (encoded) features determine where in the cortex this active representation is processed and preserved. For sensory features, activated areas are assumed to be the same as, or adjacent to, the brain areas involved in perceiving a stimulus (i.e. primary sensory cortex). In contrast, non-sensory features (e.g. semantic, phonological, phonetic) are likely to be represented in association cortices.

The central executive of Cowan's model may be localized to frontal areas, especially the dorsolateral prefrontal cortex (Cowan, 1995), just as it is in the Multiple-Component Model. However, Cowan's model affords an alternative explanation for the contributions of inferior parietal cortex and Broca's area to working memory. Specifically, the inferior parietal cortex may act to support *attentional scanning* by focusing and shifting attention across activated memory representations. In verbal maintenance tasks, some of these activated memory representations may be generated or contained within Broca's area. Thus, Broca's area may serve as a general source of phonological representation and processing. We speculate that this phonological information may be used in a variety of ways: it may be the focus of a Cowan-like attentional scanning operation, it may support speech-based rehearsal processes, and it may also support performance of non-mnemonic language tasks.

8. Does parietal cortex support attentional scanning?

Viewing inferior parietal cortex as an attention controller, rather than as a phonological store, is perhaps the most salient functional anatomical distinction that can be made on the basis of Cowan's and Baddeley's models (McElree, 2001). Using the framework provided by Cowan's model, the parietal cortex can be thought of as an attentional 'spotlight' that serves to shift and engage the focus of attention onto active representations located elsewhere in the cortex (though the spotlight metaphor may not be completely suitable; Cowan, 1995). Notably, assuming such a role for parietal cortex in attentional scanning provides an interpretation that is generally consistent with a large body of findings linking parietal areas to attentional function (Corbetta et al., 1998; Corbetta, Miezin, Shulman, & Petersen, 1993; Desimone & Duncan, 1995; Posner & Petersen, 1990). We argue below that this novel perspective on the role of parietal cortex in working memory is useful, though we acknowledge the fact there is debate in the neuroimaging and neurophysio-logical literatures about the precise attentional operations supported by parietal cortex (Corbetta, Kincade, & Shulman, 2002; Posner, 1987; Vandenberghe et al., 2000) and only recently has evidence emerged suggesting that the contributions of this region extend beyond the spatial domain (Cabeza et al., 2003; Coull & Frith, 1998; Rushworth, Nixon,

Renowden, Wade, & Passingham, 1997; Shapiro, Hillstrom, & Husain, 2002; Wojciulik & Kanwisher, 1999).

By assuming that the left parietal cortex is responsible for attentional scanning, a number of findings that resist interpretation under the Baddeley model are explained. Recall that the behavior of parietal cortex failed to exhibit four properties that might be predicted based upon Baddeley's notion of phonological storage: (1) parietal activation is not specific to verbal maintenance, (2) working memory, but not passive-listening, tasks produce activation in parietal cortex, (3) activation in parietal cortex is insensitive to phonological similarity, and (4) parietal activation sometimes fails to persist across a delay interval. Rethinking parietal activity as being related to attentional scanning provides an account in which these apparent discrepancies are resolved. The attentional scanning process of Cowan's model is domain general. Therefore, the attribution of this function to a material-independent processing region (the dorsal supramarginal gyrus) is completely consistent with neuroimaging evidence that left parietal activation can be found with both verbal and non-verbal working memory tasks; while we focus on left parietal cortex, a similar explanation could be posited for material-independent activation that is observed in the right parietal cortex. It is also clear why passive listening tasks may not activate this region (Petersen et al., 1988), as they have no specific requirement that the focus of attention be moved (usually the stimuli are presented from a single channel). Similarly, phonological similarity effects should have no selective impact on a general attentional process. Finally, failures to observe sustained delay-interval activity in parietal cortex can be understood by recognizing that, as posited in Cowan's model, speech-based rehearsal may be used in place of attentional scanning to support the maintenance of information in certain contexts. When attentional scanning is employed it should be an ongoing process expected to produce sustained parietal activation across a delay interval; however, when attentional scanning is not in use, minimal parietal activity should be expected.

Placing the focus of attention into the inferior parietal cortex also provides a novel perspective on a range of additional neuroimaging findings. For example, Cowan assumes that the attentional focus must be shared between external stimuli and internal representations. Therefore, parietal activity found in a working memory task should overlap with that in a task requiring covert attentional shifts to external stimuli. In a recent neuroimaging study, LaBar, Gitelman, Parrish, and Mesulam (1999) found precisely this pattern. To be specific, when activation observed during the performance of a working memory task was compared within-subjects (through conjunction analysis) to activation observed during performance of a non-mnemonic covert spatial attention task, the most prominent area of overlapping activity was the dorsal supramarginal gyrus. Similarly, in contrast to the expected absence of parietal activity during passive listening, auditory stimuli producing an automatic attentional (orienting) or dishabituating response might be expected to activate this region. Indeed, some recent studies have implicated the inferior parietal cortex in such automatic attentional responding (Clark, Fannon, Lai, & Benson, 2001; Downar, Crawley, Mikulis, & Davis, 2002; Kiehl & Liddle, 2001; though see Corbetta, Kincade, Ollinger, McAvoy, & Shulman (2000). Finally, Cowan (1995) notes that increasing the associations between items in memory, through repeated exposure or practice, allows search to become more efficient (McCauley, Kellas, Dugas, & DeVellis, 1976). Therefore, the observation that supramarginal gyrus activity decreases following

repeated working memory task trials using the same stimuli (Jansma, Ramsey, Slagter, & Kahn, 2001) is further consistent with its proposed role in the search process.

9. Attentional scanning versus speech-based rehearsal

As we noted earlier, Cowan acknowledges that attentional scanning is only one way in which verbally coded items may be reactivated in memory, while speech-based rehearsal serves as another. Accordingly, neuroimaging evidence for the dissociation of these two disparate reactivation processes should be obtainable. In other words, if two alternative strategies exist, the preferential use of one strategy over the other should be reflected in differential patterns of brain activity. To understand which situations are most likely to engage particular covert reactivation strategies, we can speculate on the relative benefits of each. Rehearsal is thought to be slow relative to attentional scanning (Clifton & Tash, 1973; Landauer, 1962; Sternberg, 1975), and to place fairly heavy demands on the capacity-limited central executive (Baddeley, 1986). However, rehearsal may lead to strong reactivation of each item, and may facilitate the maintenance of order information (Baddeley, 1986; Henson, 1999). In contrast, attentional scanning may be fast and efficient, but may impart only small activation increments and limited information about item ordering (Cowan, 1995; Sternberg, 1975). Rehearsal should therefore be preferred when tasks require high levels of activation at the time of retrieval (e.g., recall tasks), when order information is demanded (e.g., serial retrieval tasks), and when residual activity from earlier trials is likely to interfere with task performance (e.g. conditions with high proactive interference). Alternatively, attentional scanning should be preferred whenever rehearsal is unnecessary, because it is both faster and less capacity demanding. Some existing neuroimaging evidence seems to support these predictions.

As mentioned earlier, left inferior parietal activity is found less reliably in neuroimaging studies using recall procedures than in those using recognition procedures. One simple approach to understanding the difference between recall and recognition is to assume that recognition of items in memory is possible based on low levels of activation, while recall requires higher levels of activation (Jacoby, 1991; Kintsch, 1970; Mandler, 1980). Accordingly, minimization of parietal contributions during recall tasks may be explained by the emphasis that these tasks place on the speech-based rehearsal process needed to sufficiently reactive items above the recall threshold.

Another recent study conducted by Henson, Burgess, and Frith (2000) reported within-subject findings consistent with a tradeoff between rehearsal and attentional scanning processes. Subjects in this study performed both a standard delayed-item recognition task, in which a single item was given as the probe (item probe), and also a modified version of the task in which all trial items were included in the probe but their correct serial order had to be verified (sequence probe). When the letter probe condition was subtracted from the sequence probe condition, a left premotor region, presumably mediating rehearsal, was revealed. This difference is to be expected given the requirement for order information, and therefore rehearsal, only in the sequence probe. When the opposite subtraction was conducted (letter probe minus sequence probe) a left supramarginal region was identified.

Based on the current discussion, increased activity in the left supramarginal gyrus can be explained by the selection of the faster and less capacity demanding attentional scanning strategy to support the simple recognition judgments of the letter probe task.

10. What is the role of Broca's area?

Such neuroimaging results would seem to suggest that activation in inferior parietal cortex can serve as a marker for subjects' preferential use of attentional scanning over speech-based rehearsal. This leads us to another question: can activation within Broca's area serve as a marker of a speech-based rehearsal strategy? Broca's area certainly appears to contribute to a speech-based rehearsal process, as evidenced by the fact that Broca's area is reliably active during studies of verbal working memory and by the fact that damage to this area can lead to an apparent loss of the ability to perform speech-based rehearsal during verbal working memory tasks. However, Broca's area seems to remain active under conditions that should lead subjects to abandon speech-based rehearsal (e.g. fast presentation rates, Coull et al. (1996); running span tasks, Postle et al. (2001)), leading us to speculate that it contributes to the maintenance of information when either an attentional scanning or a speech-based rehearsal strategy is employed. This idea is consistent with Cowan's assertion that both rehearsal and attentional scanning act on phonological representations within long-term memory. In other words, if Broca's area contributes to the representation of, or access to, some type of phonological knowledge (Demonet et al., 1992; Poldrack et al., 2001; Shewan, 1980), then both attentional scanning and rehearsal strategies could be associated with activation in this area.

11. Broca's area contributions to non-mnemonic language tasks

Such broadening of the role of Broca's area explains why it is also common to find non-mnemonic tasks that produce robust activation within Broca's area. Tasks that require subjects to generate phonological representations for visually presented non-words (e.g. 'floop') provide an illustrative example. Broca's area is reliably active when subjects read pronounceable non-words (Brunswick, McCrory, Price, Frith, & Frith, 1999; Herbster, Mintun, Nebes, & Becker, 1997; Newman & Twieg, 2001), and subjects with damage to this area can exhibit selective deficits in non-word reading (phonological dyslexia, see Fiez & Petersen, 1998). Further evidence for a shared process between working memory and non-word reading comes from two other sources. First, neuroimaging studies reveal an overlap between the region within Broca's area that shows non-word effects during reading and a region that shows enhanced activity when subjects attempt to retain a set of non-words as compared to words in verbal working memory (Chein & Fiez, 2001; Fiez et al., 1996). Second, neuropsychological studies indicate that subjects with phonological dyslexia can have reduced working memory spans (Bub, Black, Howell, & Kertesz, 1987; Sasanuma, Ito, Patterson, & Ito, 1996). In fact, it has been claimed that phonological dyslexia is best characterized as a general breakdown in phonological processing rather than as a specific deficit in reading (Farah, Stowe, & Levinson, 1996; Patterson, Suzuki, &

Wydell, 1996). Similarly, it has been claimed that subjects with rehearsal-related deficits have a range of problems with phonological processing that extend beyond deficits in working memory (Martin, Breedin, & Damian, 1999; Vallar, Di Betta, & Silveri, 1997; Waters & Caplan, 1995). Importantly, the activation within Broca's area during non-word processing is not readily explained as a reflection of the use of a speech-based rehearsal strategy, since subjects retain the ability to make pseudohomophone judgments (e.g. does the non-word 'waige' sound like a real word?) under conditions of concurrent articulation (Besner, 1987; Coltheart, Avons, & Trollope, 1990; Richardson, 1987).

Interestingly, the idea that Broca's area provides a general phonological coding process that is common to both working memory and reading is at odds with a view typically forwarded by Baddeley and colleagues. Specifically, based on the absence of concurrent articulation effects in tasks such as pseudohomophone judgment, Baddeley and colleagues have argued that orthographic information is recoded and rehearsed during working memory task performance through processes that are independent of those used to recode orthographic information during reading (Gathercole & Baddeley, 1993). If concurrent articulation does not impair reading, then this task must not use processes contributed by Broca's area—the traditional marker of rehearsal. In our view, however, such conclusions rest upon the invalid assumption that concurrent articulation disrupts all of the processes engaged by speech-based rehearsal. Instead, we speculate that concurrent articulation may selectively disrupt processing in pre-SMA or the cerebellum (areas that tend to co-activate with Broca's area during verbal working memory tasks), while leaving processing within Broca's area intact. This alternative view is generally supported by indications that, in contrast to Broca's area, the cerebellum activates with simple repetitive speech tasks (Ackermann, Wildgruber, Daum, & Grodd, 1998; Fiez et al., 1996; Wildgruber, Ackermann, & Grodd, 2001) and is sensitive to increases in articulatory word length (Chein & Fiez, 2001).

We suggest, therefore, that joint activation within Broca's area and the cerebellum is necessary to demonstrate use of a speech-based rehearsal strategy, but activation of either region in isolation is insufficient. That is, activation in Broca's area may be indicative of speech-based rehearsal, attentional scanning, or non-mnemonic phonological processing, while activation in the cerebellum may be indicative of articulatory processing that supports either rehearsal or non-mnemonic aspects of overt or covert speech.

12. Links between working memory and sentence comprehension

These proposed associations between Broca's area and phonological processing, and the cerebellum and concurrent articulation effects, offer a novel perspective on the relationship between working memory and another domain of language research, sentence comprehension. A coarse distinction can be made between sentence processing theories that assume a role for working memory in comprehension (Clark & Clarke, 1977; Kintsch & van Dijk, 1978) and those that do not (Howard & Butterworth, 1989). Research backing the former view has argued that the working memory system may support comprehension by retaining a verbatim 'backup' representation that can be consulted during later processing (Baddeley, Vallar, & Wilson, 1987; Caramazza, Basili, Koller, & Berndt,

1981; Saffran & Marin, 1975; though see Caplan & Waters, 1999). This view has been elaborated within the context of Baddeley's model by claiming that the verbatim representation is created and maintained via the phonological loop (Baddeley, Eldridge, & Lewis, 1981).

Such verbatim representations do not appear to be necessary for the processing of simple sentences, since their comprehension is largely unaffected by either concurrent articulation (Baddeley, 1978; Waters, Caplan, & Hildebrandt, 1987) or phonological similarity (Baddeley & Hitch, 1974). However, activity in Broca's area is reliably found when subjects are engaged in even simple sentence comprehension tasks (Dapretto & Bookheimer, 1999; Just et al., 1996; Michael, Keller, Carpenter, & Just, 2001). We speculate that this activation once again reflects the engagement of processing that is shared by verbal working memory and comprehension, but which is not reflective of speech-based rehearsal. In other words, simple sentence comprehension and working memory may make use of shared processes and representations, but this does not mean that simple sentence comprehension involves verbal working memory or speech-based rehearsal per se.

The connection between sentence comprehension and working memory may be different for complex sentences. Processing of complex sentences (e.g. containing center-embedded clauses) is disrupted by concurrent articulation (Baddeley et al., 1981; Waters et al., 1987), and phonological similarity can affect complex sentence comprehension (MacDonald et al., unpublished data). Neuroimaging studies that have contrasted simple versus complex sentence reading (Caplan, Alpert, & Waters, 1998, 1999; Just, Carpenter, Keller, Eddy, & Thulborn, 1996; Keller, Carpenter, & Just, 2001; Roder, Stock, Neville, Bien, & Rosler, 2002; Stromswold, Caplan, Alpert, & Rauch, 1996) provide insight into the neural mechanisms that may underlie the behavioral differences between processing of these sentence types. A highly consistent result across these studies is that Broca's area is engaged to a greater degree during the processing of complex sentences than during the processing of simple sentences (e.g. all six cited studies yield this finding). Findings regarding the left dorsal supramarginal gyrus are also consistent, but in the opposite direction. Specifically, no studies report differential activity in this parietal region at different levels of complexity.

What do these findings reveal about the role of working memory in language comprehension? Under the interpretation typically derived from Baddeley's model, the absence of left parietal (dorsal supramarginal) activity in either simple or complex sentence processing tasks would suggest no use of the phonological store, and thus no verbal maintenance, in any aspect of sentence processing. Instead, we suggest that the absence of parietal activity should be interpreted as evidence that *attentional scanning* is not critically involved in language comprehension. We note, however, that this interpretation provides little explanation for the deficits in both working memory and complex sentence comprehension shown (inconsistently) by patients with ventral parietal damage (Smith & Geva, 2000). Meanwhile, the results do indicate that activity in Broca's area intensifies with increasing complexity. Although this finding is generally used to support claims that Broca's area plays a direct role in syntactic processing and representation (Caplan et al., 1998), we propose that another interpretation warrants consideration. Specifically, that the emergence of suppression and similarity effects is

an indication that subjects invoke a speech-based rehearsal strategy for complex sentence processing that is partially reflected by an activity increase in Broca's area.

If this hypothesis is correct, then based on our earlier conclusions, we would also predict that increases should also be seen in the cerebellum (and/or the pre-SMA and premotor cortex) during complex sentence processing. While available neuroimaging findings do not provide specific support for this prediction, this may reflect the fact that most studies of syntactic complexity have used either a region-of-interest approach to data analysis or a scanning procedure with limited field of view that precluded assessment of cerebellar patterns. However, cerebellar involvement in complex sentence processing is suggested by the results of a study by Papathanassiou et al. (2000), which reported cerebellar activity when subjects listened to factual stories (that presumably contained some complex sentences). Moreover, neuropsychological work (Molinari, Leggio, & Silveri, 1997; Silveri, Leggio, & Molinari, 1994) indicates that patients with cerebellar damage can exhibit agrammatism, an inability to process the grammatical structure of sentences.

So, rethinking the nature of regional processing allows us to circumvent the conclusion that working memory and sentence comprehension are independent, and to recognize instead that they may be related in two important ways. First, sentence processing and working memory may share the phonological resources provided in Broca's area. Second, complex sentence comprehension may additionally commandeer the maintenance properties of working memory through speech-based rehearsal, in order to support retrospective analysis of sentence constituents.

13. General conclusions

Both the Multiple-Component Model and the Embedded-Processes Model make empirical claims based on their paradigm of working memory. Unfortunately, neither model has been rigorously tested to determine if its components are anatomically represented. Instead, neuroimaging researchers have generally assumed that working memory is accurately portrayed by the multiple-component model, and have interpreted their findings almost exclusively in the context of this model. We have demonstrated, however, that some neuroimaging results, which are inconsistent with simple predictions derived from the multiple-component model, are explained more readily by Cowan's embedded-processes model.

Cowan's model offers the opportunity to reconceptualize the mappings between working memory processes and their neural substrates in three important respects. First, Cowan proposes an attentional scanning procedure that relies upon internal shifts of attention. We have shown that patterns of activation within the inferior parietal cortex are consistent with such a function. Second, Cowan posits that attentional scanning is only one potential strategy for maintaining information in working memory, while speech-based rehearsal is a second strategy. We argue that patterns of activation within the inferior parietal cortex can serve to detect the employment of attentional scanning over speech-based rehearsal strategies. At the same time, we speculate that there may be other areas whose activation may serve to signal the use of speech-based rehearsal over attentional

scanning strategies; such as the cerebellum. Third, Cowan places the representations that support the maintenance of information within the long-term memory system in distributed cortical regions. We argue that this offers a way to reconcile otherwise contradictory findings within Broca's area. Specifically, activation of Broca's area may be necessary, but not sufficient, evidence for speech-based rehearsal. This region may generally support both the encoding and the reactivation of phonological information, and may thus be utilized during attentional scanning, speech-based rehearsal, and a wide range of other tasks that draw upon phonological processes.

By offering this alternative perspective regarding the nature and neural instantiation of rehearsal and storage, Cowan's model also speaks to larger issues in the domain of language processing. By conceiving of working memory as dependent on representations in long-term memory that are activated by ongoing cognition, rather than as a dedicated short-term store, it is clear why activity during verbal working memory tasks overlaps neuroanatomically with activity in non-mnemonic language tasks, in that they likely utilize similar verbal representations. We have suggested, for example, that the presence of Broca's area activity in a reading task can be explained by its use of verbally specific representations, rather than by its use of a speech-based rehearsal process. Furthermore, by assuming that multiple covert reactivation strategies can be employed to support verbal maintenance, it becomes clear that the absence of activation in one part of the working memory network during performance of a language task does not necessitate the absence of a working memory contribution to the task. Thus, understanding that the parietal cortex plays an attentional role in working memory, rather than a role in phonological storage, allows for the possibility that complex sentence processing may still utilize working memory by engaging speech-based rehearsal.

Although we have shown that the Embedded Processes Model provides a successful framework in which to interpret a wide range of findings, it is important to recognize that there are many other models that could prove equally useful for understanding the neural basis of working memory and its links to language. Our intent, therefore, is not to suggest that the tenets of Cowan's model should be accepted whole-cloth, as has been done with Baddeley's model, but to show that there is utility in considering the range of theoretical constructs that are offered by alternative models. Importantly, several issues remain unresolved even under the account we have derived from Cowan's model, such as why patients with lesions in posterior perisylvian cortex exhibit working memory deficits that appear to relate to storage function (for further discussion on this issue see Ravizza et al., submitted for publication). Still, we are optimistic that by exploring alternative theoretical models it will be possible to use neuroimaging to move beyond oversimplified notions regarding the nature of processing in the brain, and to reach a unified account that reconciles a wide range of seemingly incompatible behavioral, neuropsychological, and neuroimaging findings in the domains of working memory and language.

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