

Working memory retention systems: A state of activated long-term memory

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Abstract: High temporal resolution event-related brain potential and electroencephalographic coherence studies of the neural substrate of short-term storage in working memory indicate that the sustained coactivation of both prefrontal cortex and the posterior cortical systems that participate in the initial perception and comprehension of the retained information are involved in its storage. These studies further show that short-term storage mechanisms involve an increase in neural synchrony between prefrontal cortex and posterior cortex and the enhanced activation of long-term memory representations of material held in short-term memory. This activation begins during the encoding/comprehension phase and evidently is prolonged into the retention phase by attentional drive from prefrontal cortex control systems. A parsimonious interpretation of these findings is that the long-term memory systems associated with the posterior cortical processors provide the necessary representational basis for working memory, with the property of short-term memory decay being primarily due to the posterior system. In this view, there is no reason to posit specialized neural systems whose functions are limited to those of short-term storage buffers. Prefrontal cortex provides the attentional pointer system for maintaining activation in the appropriate posterior processing systems. Short-term memory capacity and phenomena such as displacement of information in short-term memory are determined by limitations on the number of pointers that can be sustained by the prefrontal control systems.

Keywords: coherence; event-related potentials; imaging; long-term memory; memory; short-term memory; working memory

1. Introduction

1.1. History of the working memory model

Working memory refers to the collection of cognitive systems that maintain task-relevant information in an active state during the performance of a task. It functions as a work-space in which recently acquired sensory information and information from long-term memory are processed for further action (e.g., storage, computation, decision-making). The construct of working memory evolved from previously developed models of memory systems that postulated a distinct short-term store, such as Atkinson and

Shiffrin's (1968) modal model wherein the short-term memory system receives input from sensory stores and transfers information to and from long-term stores. Although the modal model accounts for a number of empirical results, it does not provide an accurate account of how short-term and long-term memories interact, nor does it correctly predict performance for certain dual-task experiments or provide an adequate explanation for the memory performance of amnesiacs. In their seminal and influential model of working memory, Baddeley and Hitch (1974) resolved many of these shortcomings by postulating a multi-component working memory system consisting of a central

executive that controls conscious processing, with access to a pair of subsystems that temporarily store phonological and visuo-spatial information. Baddeley (2000) recently revised this model, postulating a third short-term storage subsystem: an episodic buffer that forms an interface between the short-term phonological store, the short-term visuo-spatial store, and long-term memory. The episodic store augments working memory storage capacity, holding inte-

grated material such as scenes and events. The central executive is regarded as a controller of deployment of attention, with no storage capacity. A key aspect of Baddeley's model is that the various subsystems draw on different processing resources and can, to some extent, function independently of each other.

A number of other models of working memory have been proposed since the initial Baddeley and Hitch (1974) paper. Most of the models, though not all, share Baddeley's view of multiple subsystems and temporary stores based on modality-specific codes (see Miyake & Shah 1999, for discussions and comparisons of various current models of working memory). An important distinction among the conceptualizations of working memory is in how short-term storage is implemented and how it is related to long-term memory. Baddeley (1986; 2001a; 2002) posited that the working memory short-term storage modules are separate from long-term memory storage modules. This view is based on neuropsychological dissociations between performance on tasks involving either primarily short-term memory or primarily long-term memory resources. Baddeley and Logie (1999) suggested that information not accommodated by the working memory short-term stores (e.g., lexical and semantic information in verbal working memory) contributes to working memory performance via activation of representations in long-term memory. Hulme et al. (1997) and Saint-Aubin and Poirer (1999) further articulated this idea, proposing that lexical and semantic contributions to serial recall in verbal short-term memory are via a redintegration process that reconstructs degraded phonological codes during retrieval.

1.2. Short-term memory as activated long-term memory

Investigators such as Crowder (1993) and Cowan (1995; 1999; 2001) have been proponents of a contrasting view of short-term memory operation, namely, that long-term memory and short-term memory are different states of the same representations, with activated representations in long-term memory constituting all of short-term memory. Based on findings such as the occurrence of serial position and recency effects in both short-term and long-term memory tasks, Crowder (1993) argued that short-term memory and long-term memory follow similar rules and hence there is no reason to postulate separate long-term and short-term storage systems. In Crowder's view, memory storage takes place in the same neural structures in which the information was initially processed. Fuster (1995; 1997) has taken the same proceduralist position, based on observations of single neuron activity in primates during short-term memory tasks. Fuster (1995) commented that we are dealing with "the *memory of systems, not . . . systems of memory.*" Cowan's (1988; 1995; 1999) views are similar to Crowder's, with short-term memory stores constituted by an activated subset of long-term memory. Cowan argued for the construct that short-term memory involves all information accessed by a task, including (1) activated memory in the focus of attention, (2) activated memory not in the focus of attention, and (3) inactive memory accessible by activated retrieval cues. Short-term auditory-sensory memory processes in experiments involving presentation of multiple streams of stimuli are examples of the latter two types of activation (Cowan 1984; 1995). Deployment of attention is a crucial feature of Cowan's model of short-term memory,

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with attention sustaining and limiting the activation of long-term memory. In Cowan's (1999) model the capacity limitation of short-term memory is due to the limited capacity of the focus of attention.

With respect to the role of sensory information in short-term memory, Penney (1989) hypothesized that verbal short-term memory involves, in addition to phonological codes, contributions from modality-specific auditory and visual codes. A number of lines of evidence support Penney's view: (1) memory is improved when different items are presented in different modalities in contrast to when all items are presented in the same modality; (2) recall is enhanced when items are organized by modality as compared to their being organized by time of presentation; and (3) two concurrent verbal tasks can be performed more effectively when different input modalities are used than when only one input modality is used.

Baddeley (2001a) claimed that construing short-term memory as activated long-term memory is inconsistent with neuropsychological data because there are individuals with long-term memory deficits but not short-term memory deficits, and individuals with short-term memory deficits but not long-term memory deficits. However, Cowan (1999) has argued that long-term memory deficits are not necessarily due to damaged stores. Rather, such deficits can be due to impaired binding processes involving hippocampal-neocortex connections responsible for eliciting simultaneous activations across long-term stores that lead to an episode being stored (Rickard & Grafman 1998). Activation of the individual stores that accompany short-term retention of information can be preserved in amnesia.

With regard to patients with short-term but not long-term memory deficits, Vallar and Baddeley (1984) reported an individual whose span in verbal serial-recall tests was below the normal range, but whose performance on word learning, paired-associates learning, and short-story learning tests was within the normal range. The poor span in serial recall was attributed to an impaired phonological short-term store. Although Baddeley (2001a) interpreted these results as evidence for distinct short-term and long-term phonological stores, the normal performance on the learning tests of long-term memory may have been due to lexical, semantic, and syntactic processes invoked by the learning tasks which compensated for the impaired phonological processing. Nevertheless, if verbal short-term memory representations are indeed activated verbal long-term memory representations, then deficits in verbal short-term memory for specific types of representations should be indicative of impairments in establishing long-term memories for those representations. Romani and Martin (1999) reported that individuals with a semantic short-term memory deficit also have difficulty forming semantic but not phonological long-term memories, whereas individuals with a phonological short-term memory deficit show the reverse pattern of difficulty. Therefore, when the nature of the representations is taken into account, the neuropsychological evidence for distinct short-term and long-term memory stores is not compelling.

1.3. Episodic memory

Although activation of long-term memory representations of items contributes to their retention in short-term memory, it does not account for all aspects of the retention

process. Serial recall of the order of events involves conjunctions of representations that are not likely to be retained and recalled by activation of the representations alone. Both Cowan (1995; 1999; 2001) and Baddeley (2000; 2001a) proposed that retention of serial-order information involves the formation of new episodic links between the activated representations of items held in short-term memory. Baddeley (2001a) further argued that there is a distinct short-term store for episodic links, citing a functional magnetic resonance imaging (fMRI) study by Prabhakaran et al. (2000) as providing neural evidence of such a store. Prabhakaran et al. found greater activation in the right prefrontal cortex when integrated (i.e., requiring binding of individual items) rather than unintegrated visual stimuli were used in a short-term memory task. The authors claimed that this was evidence of a buffer for the temporary retention of integrated information. We suggest that a more precise interpretation of the fMRI data is that the right prefrontal cortex participates in the process of maintaining binding information in an active state. Whether there is a separate store for binding information or whether the binding "representations" are based on the same neural structures that, with consolidation, become part of the long-term memory representations for the bindings, is an issue that was not resolved by Prabhakaran et al.'s findings. Our view is that the neural connections underlying the binding processes that produce episodic links are the basis for both short-term and long-term episodic memory. Recall and maintenance of episodic information involves activation of the binding circuitry; retention of novel episodic information involves the operation of binding formation and the initial consolidation process. In either case, the same neural connections are involved.

1.4. Scope of reviewed research supporting activation models of short-term memory

In contrast with Baddeley's claim that short-term and long-term memory stores are distinct, this article argues for the view that short-term memory corresponds to activated long-term memory and that information is stored in the same systems that initially processed the information. On theoretical grounds, activation-proceduralist models have the advantage of parsimony over models that postulate distinct short-term and long-term memory stores. On empirical grounds, electrophysiological and hemodynamic imaging data from normal, intact humans substantiate activation models. These data are reviewed in this article.

Research into short-term memory has used cognitive experiments, studies of patients, and functional neuroimaging techniques to motivate an understanding of both how information is retained over short periods of time and which brain areas are crucial for encoding, retaining, and retrieving information held in short-term memory. What has been lacking in these studies is accurate information regarding the timing and duration of the various processes enlisted in short-term memory operations. Hence, in this article we concentrate on studies that employed high temporal resolution event-related potentials (ERPs) to provide information about the timing of brain processes involved in short-term memory operations. Such studies make available unique and novel information on the mechanisms employed in active maintenance and on how networks involved in short-term storage operations map onto networks

involved in the perception, encoding, and determination of meaning. We also review hemodynamic imaging studies that provide key anatomical information that complements the ERP findings. Results of these various studies are most compatible with models of short-term storage operations that focus on sustained activation of the perceptual and associated long-term memory systems involved in the initial bottom-up processing of information, and posit an important role for attentional systems in the maintenance process (e.g., Cowan 1999), as opposed to models that emphasize buffers based on neural systems that are specialized for short-term storage (e.g., Baddeley & Logie 1999).

Lesion and hemodynamic imaging investigations have produced abundant converging data on the location of brain regions that contribute to short-term memory operations (Cabeza & Nyberg 1997; 2000; Smith & Jonides 1999; Vallar & Papagno 1995; Vallar et al. 1997). The data have consistently supported models of short-term memory that are based on multiple subsystems and modality-specialized temporary stores. In this context, we note that findings of multiple, modality-specialized short-term stores are fully compatible with the position that short-term memory corresponds to activated long-term memory representations, given that long-term memory involves multiple, modality-specialized stores.

Tasks that entail manipulation of information and updating memory – functions of the postulated central executive – evidently involve multiple sites in the frontal cortex (D'Esposito et al. 1995; Manoach et al. 1997; Owen 1997; Postle et al. 1999). Encoding and storing phonological information involve left parietal and left frontal regions that underlie language processing and speech production (Awh et al. 1995; 1996; Henson et al. 2000; Jonides et al. 1998; Paulesu et al. 1993), whereas encoding and storing visuo-spatial information engage ventral (inferior temporal cortex) and dorsal (posterior parietal cortex) visual processing pathways involved in perceptual processing (Awh & Jonides 2001; Courtney et al. 1996; 1997; Haxby et al. 2000; Jonides et al. 1993). Such studies have been very useful in mapping the cognitive architecture of human short-term memory to specific brain regions. However, the capability of hemodynamic imaging to provide direct, detailed information on the timing of neural processing underlying the operation of short-term memory is limited because hemodynamic responses can be substantially delayed and prolonged in comparison with neural and behavioral responses.

The complementary approach of using high temporal resolution techniques such as electroencephalographic (EEG) and magnetoencephalographic (MEG) recordings from the scalp can be useful when dealing with timing issues. Although the capability for determining the locations of brain activation from scalp recordings is limited, EEG and MEG recordings can provide real-time measures of brain activity with submillisecond accuracy. ERP data extend knowledge gained from hemodynamic imaging studies by providing detailed tracking of the time-course of brain activation across encoding, retention, and retrieval phases of an eliciting event. With ERP data, long duration, sustained processes can be distinguished from short, limited duration transient processes. Additionally, by comparing rapid fluctuations in EEG recordings from multiple sites, EEG coherence analysis yields information on the degree of neural synchronization between brain regions within a specific time interval and frequency band. EEG

coherence measures provide an approach for investigating interactions among brain regions during short-term memory operations, thereby further extending knowledge gained from ERP studies. Issues such as whether cognitive processes that operate in parallel actually interact can be best addressed by coherence methods.

The ERP studies we consider in this article usually employed either delayed match-to-sample or delayed serial-recall paradigms, with delay intervals in the range of 3,000–4,000 msec. The strategy in these studies was to manipulate the type or amount, or both, of information held in short-term memory and test whether the manipulation produced differences in brain activity during the delay interval. Differences in the delay interval of ERP timing or amplitude as a function of the information held in short-term memory indicate that brain activity during retention is sensitive to such information. Finding that brain activity during retention is influenced by the type of information held in short-term memory is interpreted as evidence that the information is being held in an active state during retention. Variation of ERP scalp topography as a function of condition indicates that the anatomical configuration of the generators of the ERP activity differs across conditions. (A brief discussion of topography and estimation of the brain sources of scalp-recorded ERP activity is presented in the Appendix.) Consequently, variations in the delay interval of ERP topography with the manipulation of information maintained in short-term memory are interpreted as evidence that the configuration of brain systems active during retention varies with the nature of the information. Coherences between recording sites reflect the pattern and degree of connectivity between brain regions. Thus, differences between coherences as material maintained in short-term memory is manipulated, are interpreted as evidence that connectivity between brain regions active during retention is sensitive to the properties of the maintained material.

Results of the ERP studies reviewed below indicate that short-term retention processes involve sustained activation of both frontal cortical control systems and posterior cortical systems involved in perception and comprehension of visuo-spatial and linguistic information, with enhanced neural synchrony between the frontal and posterior systems during retention. They further indicate a greater diversity and specialization of retention processes than originally proposed by Baddeley and Hitch (1974). For visual stimuli, in addition to the demonstration of separate sustained storage systems for visual-object and visuo-spatial material, there is also evidence of transient, intermediate duration storage systems. For language stimuli, in addition to phonological codes, there is evidence that lexical-semantic and modality-specific codes actively contribute to the retention process, rather than contributing only during recall by reintegration. The temporal morphology of the ERPs indicate that brain regions active during initial processing (prior to the retention interval) remain active during the retention interval, supporting the proceduralist-activation models of memory proposed by Cowan (1995; 1999), Crowder (1993), and Fuster (1997). The behavior of an ERP deflection sensitive to priming indicates that consciously maintaining items in memory raises the level of activation of long-term representations of the items to a level higher than that reached by priming due to processing the items but not consciously holding them in memory. This finding

provides strong support for the notion that activation of long-term memory representations is the root of short-term memory performance. We also review complementary hemodynamic imaging studies, which provide anatomical support for proceduralist, activation models, and for the idea that the posterior cortex provides the representational basis for most short-term memory operations and the prefrontal cortex provides the attentional control.

2. Retention of visuo-spatial information in short-term memory

Numerous studies have shown that the visual system involves, beyond the primary visual cortex, separate cortical pathways for the perception of object (ventral pathway) and spatial (dorsal pathway) information (Grady et al. 1992; Hanley et al. 1991; Harter & Aine 1984; Mangun et al. 1993; Rösler et al. 1995; Ungerleider & Mishkin 1982; Van Essen et al. 1992). Both pathways include extrastriate cortex. The ventral pathway also includes inferior temporal cortex; the dorsal pathway also includes posterior parietal cortex. Results from hemodynamic studies (Smith et al. 1995) and ERP studies (Mecklinger & Pfeifer 1996; Ruchkin et al. 1997b) indicate that visual short-term memory divides along similar lines. However, findings from the fMRI studies suggest that only perceptual and transient storage operations occur in posterior visual processing pathways (Haxby et al. 2000), and that sustained storage occurs in the prefrontal cortex. In contrast, the ERP studies indicate that both transient and sustained storage operations occur in the posterior visual processing pathways. The ERP findings show that during retention there is sustained activation in brain regions underlying posterior and temporal scalp, with the amplitude of the sustained brain activity varying directly with memory load.

These results were obtained in delayed match-to-sample tasks with linear arrays of geometric objects (object task) and two-dimensional patterns of randomly placed squares (spatial task; see Mecklinger & Pfeifer 1996), or with schematic faces (object task) and the motion of an asterisk (spatial task; see Ruchkin et al. 1997b). The topographies of the scalp ERP activity in the retention interval of the Ruchkin et al. (1997b) study were sharply focused over parietal scalp in spatial tasks and more broadly distributed over parietal-to-frontal scalp in the object tasks (see Fig. 1), consistent with the sources of the scalp ERP activity during retention primarily involving the dorsal pathway for spatial information and the ventral pathway for object information. It has been further demonstrated that the patterns of ERP activity found in the retention interval of visual short-term memory tasks do not occur in control tasks that involve similar encoding and response processing, but have negligible memory demand (Low et al. 1999; Ruchkin et al. 1995).

Estimates of the locations and time courses of the brain sources of scalp-recorded ERP activity (Scherg 1990) were used to examine the timing of activation in specific brain regions during the encoding and retention of visual object and spatial information (Ruchkin et al. 1997b). The time courses of activation in primary visual cortex, posterior and anterior temporal lobes, posterior parietal cortex, and prefrontal cortex are illustrated in Figure 2. The sources that best represent activity in primary visual cortex display early phasic responses, with maximal activation during stimulus presentation and relatively little activation in the subse-

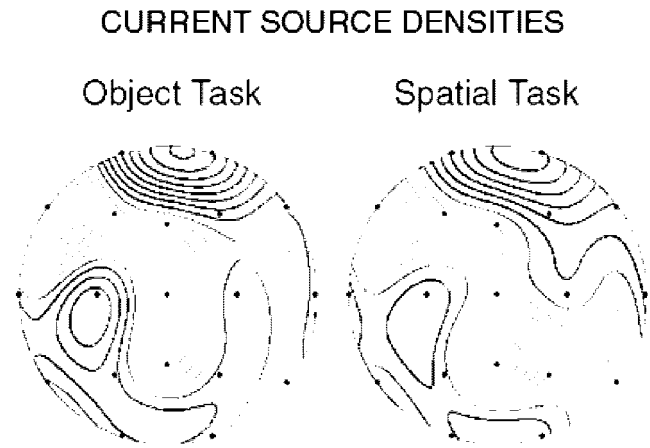


Figure 1. Estimated current source density (CSD) maps for the object and spatial tasks of the scalp topography of ERP activity at the end of the retention interval (3,010–3,550 msec after stimulus offset). The difference between contour lines corresponds to a current density increment of $1 \mu\text{V}/\text{cm}^2$. The current source densities were derived from the across-subjects averaged ERP amplitudes. Shaded areas of the maps indicate positive amplitudes and unshaded areas indicate negative amplitudes. The maps are 90° projections with the front of the head at the top. Electrode positions are indicated by the dots. The three dots in a vertical line at the center of the map correspond (from top to bottom) to midline frontal, central, and parietal scalp sites, respectively.

Note the differences along the midline between the CSD maps for the object and spatial tasks. For the spatial task, the CSD has a pronounced negative focus over parietal scalp. For the object task, the CSD negativity is broadly distributed from parietal to frontal scalp. This topographic difference indicates that the configuration of brain sources active during retention is different in the object and spatial tasks.

quent retention interval (Fig. 2, top row). Brain regions active during the retention interval are located mainly in the ventral and dorsal visual processing pathways and prefrontal cortex. For both object and spatial information, the source analysis revealed a mixture of early phasic activity during stimulus presentation followed by long duration transient activity in the posterior temporal lobes (Fig. 2, second row from top). The long duration transients began during stimulus presentation and continued into the retention interval for approximately 2,500–3,000 msec. The source analysis further indicated that there was sustained activation in both prefrontal cortex and posterior visual processing pathways during retention (Fig. 2, bottom two rows). For the object task the sustained activity was in the anterior temporal lobes (ventral pathway), and for the spatial task the sustained activity was near the junction of parietal and occipital cortex (dorsal pathway). In the object task, where all the information to be retained was available at stimulus onset, sustained activity in the anterior temporal lobe started during stimulus presentation. The spatial task required memorization of a sequence of movements, with the last movement beginning 1,500 msec after the stimulus began. In this case, sustained activity near the junction of parietal and occipital cortex did not begin until presentation of the stimulus sequence was complete. In both tasks, the onset of the sustained activity observed in the dorsal and ventral visual processing pathways was 60 to 300 msec before the onset of the sustained activity observed in prefrontal cortex.

Visual-Spatial Short-Term Memory

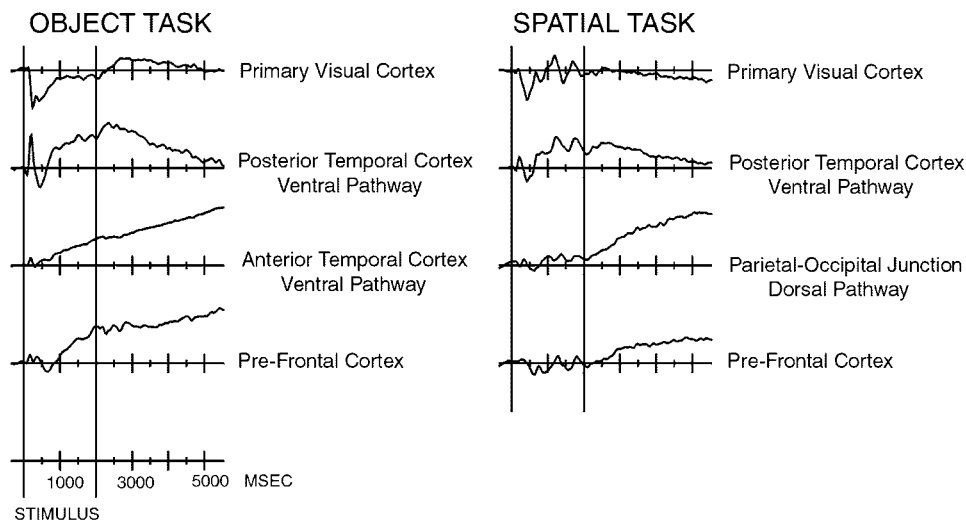


Figure 2. Estimated time courses of activation in visual cortices and pre-frontal cortex during encoding and retention of visual-object or visual-spatial information. Based upon Sperling's (1960) finding that the maximum duration of iconic memory is of the order of 1,000 msec, the estimated latency at which the mode of processing shifted from the domain of encoding to retention was approximately 3,000 msec (1,000 msec after stimulus offset). The time axis extends from 360 msec before to 5,550 msec after stimulus onset. Stimulus duration is 2,000 msec. The waveforms and their brain locations were estimated by source analyses (Scherg 1990) of across-subjects ($n=12$) averaged ERPs recorded from scalp by a 24-channel montage. The vertical scale is in arbitrary units. The stimulus presentation interval is demarcated by vertical lines. The ERPs were originally recorded with AC-coupled amplifiers (which attenuated low frequency ERP activity). The waveforms were digitally rendered to the approximate wave shapes that would have been obtained with DC-coupled amplifiers (no attenuation of low frequency ERP activity).

The source analyses indicate that primary visual cortex is most active during stimulus presentation, with relatively short latency phasic activity synchronized to the presentation of each stimulus (top row). There is sustained activity during retention in both prefrontal cortex (bottom row) and the dorsal and ventral visual processing pathways (third row from top). The waveforms in the second row from the top further indicate that long duration transient activity begins during stimulus presentation and extends for 2,000–3,000 msec into the poststimulus interval.

The analysis of brain sources indicated that maintenance of visuospatial information involves sustained activation in both prefrontal cortex and posterior visual processing systems. This finding of sustained activity in posterior cortex supports Cowan's (1995) and Fuster's (1997) views that maintaining activation in cortical regions subserving perception is a component of the retention process. Prefrontal cortex and posterior perceptual regions interact, with prefrontal cortex apparently providing the top-down control that extends activation in posterior cortex which begins during perception and encoding.

2.1. Transient visual short-term memory

The sources with transient time-courses (Fig. 2, second row from top) – brief windows of activity in the posterior temporal lobe presumably involved in intermediate visual processing operations – support Cowan's (1995) contention that visual working memory consists of at least three stages: an initial, high capacity, very limited duration iconic store that encodes the physical features of stimuli (Sperling 1960), an intermediate transient stage, and a limited capacity, postcategorical sustained short-term store. It is noteworthy that the transient stores appear to be in a part of the ventral pathway involved in the preliminary processing of visual material, but that sustained storage operations appear to be in ventral or dorsal pathway regions involved in higher level processing of visual material.

2.2. Attention-based maintenance mechanisms

The view that short-term storage of visuo-spatial information depends, at least in part, on enhanced activation in visual cortex due to attention-based maintenance mechanisms is supported by ERP studies of short-term memory and selective attention (Awh et al. 2000; Awh & Jonides 2001). In the memory task, subjects remembered the locations of three falsefont characters, all of which were in either the left or right visual field. A probe stimulus presented during the delay interval elicited a short-latency phasic response that was larger when the probe was in the same visual field as the memory-set stimuli than when the probe was in the opposite visual field. The timing and topography of the enhanced response to the probe in the memory task were very similar to the enhanced response found in a visual selective-attention task when the eliciting stimulus was in an attended location in comparison with when the stimulus was in an unattended location.

A combined PET-ERP source localization study (Hillyard & Anllo-Vento 1998) showed that enhanced ERP responses to stimuli in attended locations arise in extrastriate visual cortex, contralateral to the field of the attended stimulus. Furthermore, an fMRI study (Awh et al. 1999) that employed short-term memory and selective attention tasks similar to those in the Awh et al. (2000) ERP study found that hemodynamic activation is greatest in visual cortex contralateral to the field of the memorized or attended stimuli, with a high degree of overlap of fMRI activation in

the memory and attention tasks. This convergence of results implies that short-term storage of visual location information entails enhanced, sustained activation in cortical regions involved in the perception/encoding of the visual material, and the enhanced activation depends on attention-based maintenance mechanisms.

2.3. Summary: Visuo-spatial working memory

Implications of the ERP studies of visual working memory are summarized schematically in Figure 3. The timing of the initial (<1,000 msec post-stimulus) phasic deflections in primary visual cortex and the posterior temporal lobes suggests that these brain regions contribute to the operation of the iconic store (Fig. 3, top row). The subsequent longer duration (>3,000 msec) deflections in the posterior temporal lobes indicate the existence of transient, intermediate stores whose role may be to support the translation of information from iconic to sustained storage formats (Fig. 3, middle row). The sustained activity in the dorsal and ventral pathways indicates that short-term maintenance of visual information depends on activation of posterior sensory processing systems as well as the prefrontal cortex (Fig. 3, bottom row). This contrasts with fMRI studies of visual working memory by Courtney et al. (1997) and Haxby et al. (2000), in which activation in posterior visual processing pathways appeared to have a pronounced transient character in comparison with clear sustained activation in frontal regions. Haxby et al. suggested that the role of these posterior regions is mainly in the domain of perceptual processing, and that short-term storage depends primarily on frontal regions. The ERP findings suggest that the fMRI measures in posterior cortex may have given too much weight to the activation of the transient stores, thus cloak-

ing the sustained activity in posterior cortex and its contribution to short-term retention of visual information. The role of the frontal regions may be in the domain of sustained attentional drive directed at those posterior regions whose activation is to be maintained.

3. Retention of verbal information in short-term memory

A number of ERP studies of delayed serial recall indicate that verbal short-term memory depends on more than phonology during retention and redintegration of degraded phonological representations at retrieval. Using sustained ERP activity recorded during the retention interval, Lang et al. (1992) and Ruchkin et al. (1997a) found that retention of verbal material involves processes that are specific to the modality of presentation, and Ruchkin et al. (1999) found that sustained supramodal lexical and semantic processes also were active during retention. Finally, an item-recall study (Cameron et al. 2004) indicated that the contribution of semantic representations in long-term memory to short-term retention is not simply a result of their being primed during study of the stimuli to be memorized. Rather, the act of maintaining information in short-term memory results in a concurrent heightened activation of long-term memory representations, beyond the level of activation caused by priming associated with the initial processing of the stimuli.

3.1. Modality-specific processing streams in verbal short-term memory

Penney (1989) has argued that, along with phonological rehearsal, auditory or visual modality-specific verbal short-term memory processes support retention, depending on whether the material is heard or read, with the auditory processing stream being more durable than the visual processing stream. The results of two ERP studies (Lang et al. 1992; Ruchkin et al. 1997a) support Penney's contention. The pattern of ERP activity during the poststimulus retention interval differed for verbal material (digits in Lang et al., a nonword in Ruchkin et al.) that was heard or read. Note the differences between the ERP waveforms (Fig. 4a) and scalp topographies (Fig. 4b) associated with the two modes of stimulation in the Ruchkin et al. study.

For visual but not auditory stimuli, Ruchkin et al. (1997a) found a long duration transient positivity at midline parietal and central sites that began during stimulus presentation and ended approximately 2,500 msec after stimulus offset (Fig. 4a). The amplitude of the transient positivity increased directly with verbal memory load (Ruchkin et al. 1990; 1992; 1994). The midline posterior transient positivity was not found in ERP scalp recordings obtained in visual-object or visual-spatial short-term memory tasks (Ruchkin et al. 1992; 1994; 1995; 1997b). In view of its timing, sensitivity to memory load, and apparently exclusive elicitation by verbal material that is read, this aspect of the visual processing stream evidently indexes the operation of a visual, nonphonological verbal storage process. This process is possibly based on orthographic codes; it is active around the time of phonological recoding and it maintains representations of material that have undergone initial visual analysis (Shallice & Vallar 1990; Vallar & Papagno 1995). Sustained negative ERP activity was evident in the

Stages of Visual Short-Term Memory

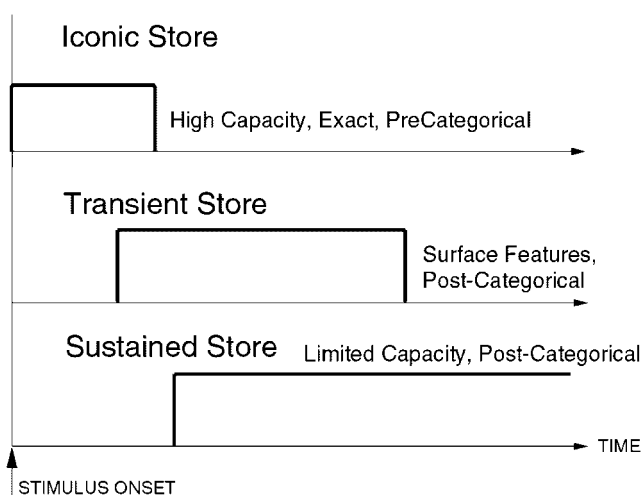


Figure 3. Schematic of the timing of the activation of three hypothesized short-term storage systems that contribute to the operation of visual short-term memory. The duration of the initial, iconic stage is about 500–1,000 msec (Sperling 1960). Based on results of ERP studies, the transient store operates over the 500–4,500 msec latency range, and the onset of the sustained store is dependent on the timing of stimulus delivery. In Ruchkin et al. (1997b), the onset of the sustained store was approximately 500–800 msec after all the information provided by the stimulus had been delivered.

(a) VERBAL SHORT-TERM MEMORY FOR MATERIAL THAT IS HEARD OR READ

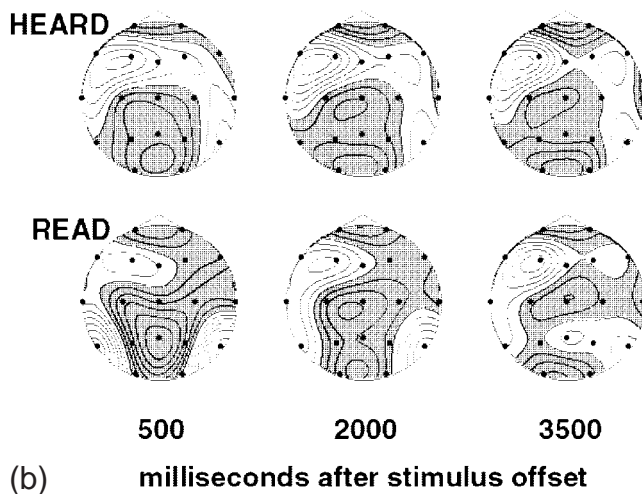
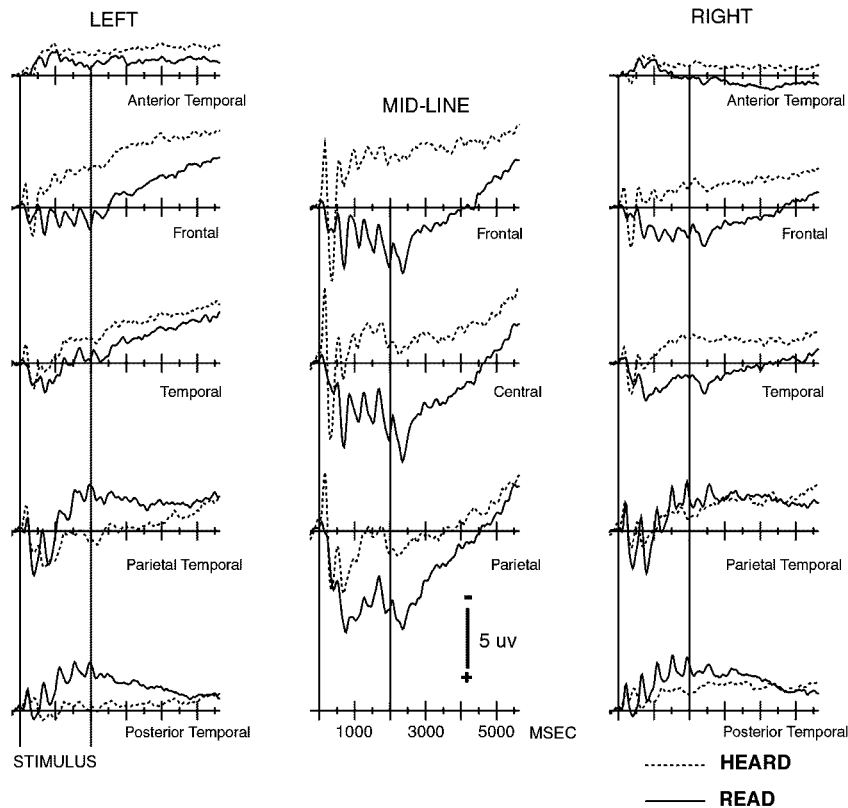


Figure 4. (a) Across-subjects ($n = 13$) averaged scalp ERPs in a delayed serial-recall task in which the material was presented either aurally (dashed lines) or visually (solid lines). The task was to remember a pronounceable five-syllable nonword. The time axis extends from 270 msec before to 5,640 msec after stimulus onset. Stimulus duration was 2,000 msec. The ERPs were originally recorded with AC-coupled amplifiers (which attenuated low-frequency ERP activity). The waveforms were digitally rendered to the approximate wave shapes that would have been obtained with DC-coupled amplifiers (no attenuation of low-frequency ERP activity). The ERPs are plotted with negative polarity up with respect to a digitally linked A1 and A2 reference. Stimulus presentation intervals are demarcated by vertical lines.

Note that for auditory stimuli there is a sustained frontal negativity, lateralized to the left, with a relatively short onset latency (during the stimulus interval). For visual stimuli, the sustained frontal negativity is lower amplitude, with a relatively late onset (after the stimulus interval). The ERPs elicited by the visual stimuli also display both a transient positivity over centro-parietal scalp, which begins during stimulus presentation and ends about

2,500 msec after stimulus offset, and a transient negativity, over bilateral posterior temporal and parietal temporal scalp. No such positivity is elicited by the auditory stimuli.

(b) Estimated current source density maps for the scalp topography of the ERP activity presented in Figure 4a. The maps are for the activity at selected time points in the retention interval: 500, 2,000, and 3,500 msec after offset of the 2,000-msec duration stimulus. The difference between contour lines corresponds to a current density increment of $1 \mu\text{V}/\text{cm}^2$. Shaded areas of the maps indicate positive amplitudes and unshaded areas indicate negative amplitudes. The maps are 90° projections with the front of the head at the top. Electrode positions are indicated by the dots. The three dots in a vertical line at the center of the map correspond (from top to bottom) to midline frontal, central, and parietal scalp sites, respectively.

Note that maps for the auditory stimuli (upper row) indicate a relatively rapid buildup of ERP negativity focused over left frontal scalp. In contrast, maps for the visual stimuli (lower row) indicate that the left frontal negative focus builds up more slowly, and that early in the retention interval there is a focus of positive activity over central-posterior scalp, and a bilateral focus of negativity over posterior temporal scalp that is not seen in the maps for auditory stimuli. These differences in timing and topography between the brain responses to auditory and visual stimuli are evidence for the contribution of modality-specific processes to the operation of verbal short-term memory.

poststimulus retention interval for both auditory and visual stimuli, however there were timing and topographic differences for the two modalities. For auditory stimuli, the sustained negativity appeared to have two constituents: a left-lateralized negativity that was largest over frontal sites and negligible over posterior sites, and a lower amplitude right-lateralized negativity with roughly the same amplitude at frontal and posterior sites. Both of these auditory sustained negativities began during the stimulus interval. The negativity elicited by the visual stimuli also appeared to have two constituents: a frontal, left-lateralized negativity, with a lower amplitude and later onset (during the poststimulus interval) than the left frontal auditory negativity, and a bilateral, transient negativity, most clearly discerned at posterior temporal sites (see Fig. 4a), that began during stimulus presentation and decreased over the poststimulus, retention interval.

The left-frontal negativity that is common to both modalities (albeit with different amplitudes and onset latencies) probably reflects operations associated with maintaining phonological representations in verbal short-term memory. Its earlier onset for auditory stimuli is evidence for auditory material having a rapid, direct access to the phonological memory system, whereas visual material undergoes a more time-consuming recoding to a phonological format before entering the phonological system through articulatory rehearsal (Shallice & Vallar 1990).

The amplitude of the left frontal negativity varies directly with verbal memory load (Ruchkin et al. 1990; 1992; 1994), and there is a significant across-subject correlation between its amplitude and articulation rate (Ruchkin et al. 1994), suggesting that phonological rehearsal operations covary with the processing indexed by the left frontal negativity. A study that contrasted retention of familiar, verbalizable material with unfamiliar, non-nameable material indicates that left frontal negativity incorporates a composite of executive control processes (Bosch et al. 2001). Taken together, these various findings suggest that the left frontal negativity indexes a combination of attentional control and phonological rehearsal operations that are involved in the short-term retention of verbal material.

The ERP data map onto Penney's view of verbal short-term memory. The left frontal negativity reflects sustained mnemonic operations – probably involving phonological representations – that are common to both auditory and visual stimuli. Modality-specific operations are indexed by the sustained negativity over the right hemisphere elicited by auditory stimuli, and the posterior transient waveforms elicited by visual stimuli, namely, the midline positivity and bilateral temporal negativity. The timing of the modality-specific ERP patterns suggests that auditory verbal mnemonic processes are more durable than visual verbal mnemonic processes.

3.2. Contributions of lexical and semantic codes to retention

Based on evidence from behavioral studies of intact and impaired subjects, there is widespread agreement that phonological codes are involved in the maintenance of verbal information in working memory (Baddeley 1986). There is less agreement about whether lexical-semantic codes actively contribute to the maintenance process. One view is that lexical-semantic codes are not actively involved in retention; rather, lexical-semantic information is thought to contribute to verbal working memory during retrieval, with

lexical-semantic codes in long-term memory facilitating recognition of partially degraded information in the phonological store (Hulme et al. 1991; 1997; Walker & Hulme 1999). Alternative views stress that language processing activates a variety of codes (modality-specific, phonological, lexical, semantic, syntactic) that are maintained at different strengths over time, depending on task demand (Martin & Romani 1994; Martin & Saffran 1997; Monsell 1984; Penney 1989; Saffran 1990; Saffran & Martin 1990). Though phonological rehearsal is a possible contributor to the maintenance of information in verbal short-term memory, it is viewed as neither necessary nor sufficient for all of the retention operations required of verbal short-term memory. Cowan (1988) and Cowan and Kail (1996) postulated that the attention given to maintaining verbal material in working memory raises and prolongs activation of the words' long-term memory codes, and, as a result of this enhanced activation process, lexical-semantic codes contribute to retention of verbal information in working memory.

It is difficult to decide between these different conceptions of verbal working memory from behavioral data alone, because behavioral data reflect a combination of encoding, retention, retrieval, and decision operations. Using the temporal resolution of ERP findings, brain activity specific to the retention interval can be delineated and analyzed, so that the types of codes that influence the retention process can be determined. This approach has been applied across a series of studies that examined the contributions of lexical and semantic processes to brain activity during retention. These studies have shown that the patterns of brain activation during short-term maintenance of verbal material are influenced by the lexical status of the material (Ruchkin et al. 1999), whether the referents of words are concrete or abstract (Ruchkin et al., unpublished data).

3.3. Lexical status

Evidence for an active contribution of lexical codes to the maintenance of verbal information in working memory was obtained from ERP data recorded during performance of a serial-recall task involving retention of aurally presented words or pseudowords designed to be maximally similar to the words in their sound structure (Ruchkin et al. 1999). The number of items in the word list (five) and pseudoword list (three) were such that recall error rates were approximately matched for the two types of stimuli. The finding that five words could be retained at approximately the same level of accuracy as three pseudowords was consistent with prior studies of verbal working memory (Hulme et al. 1991; Roodenrys & Hulme 1993). It has been argued that the cause of the advantage of words over pseudowords is that restoration during retrieval of partially degraded information in the phonological buffer is more effective for words (Roodenrys & Hulme 1993). Such processing during retrieval may contribute to the word advantage, but there is no compelling reason to believe that it is the only contributor. Lexical status also influenced ERP findings during the delay interval (3,600 msec) of the serial-recall memory task, well after stimulus presentation terminated and well before retrieval commenced, indicating that brain activity during retention is directly influenced by the availability of lexical-semantic information (Ruchkin et al. 1999). Words elicited more negativity during retention than did pseudowords, with the effect being most marked at the central midline

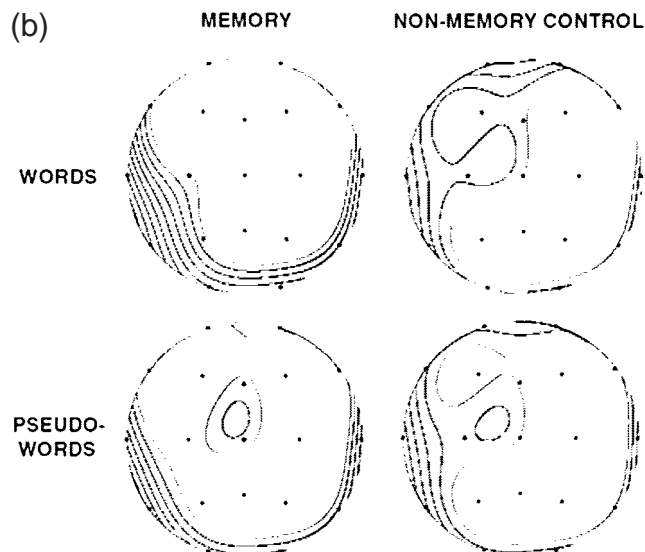
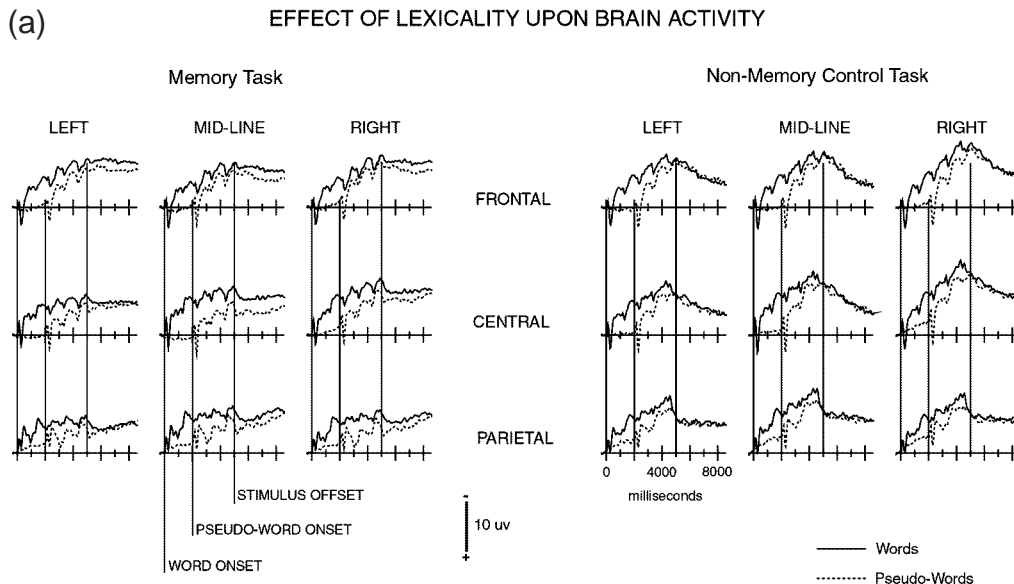


Figure 5. (a) Across-subjects ($n = 11$) averaged scalp ERPs in verbal short-term memory (left panel) and nonmemory control (right panel) tasks contrasting the processing of words (solid lines) and pseudowords (dashed lines). Stimuli were presented aurally. In order to approximately balance the error rates in the word and pseudoword memory tasks, stimuli consisted of either five words or three pseudowords. The time axis extends from 360 msec before to 8,595 msec after word onset. To align the offset times of words and pseudowords (5,000 msec after word onset), pseudoword onset was 2,000 msec after the time of word onset. The ERPs were originally recorded with AC-coupled amplifiers (which attenuated low-frequency ERP activity). The waveforms were digitally rendered to the approximate wave shapes that would have been obtained with DC-coupled amplifiers (no attenuation of low-frequency ERP activity). The ERPs are plotted with negative polarity up with respect to a digitally linked A1 and A2 reference. Stimulus presentation intervals are demarcated by vertical lines.

Note that the sustained negativity during the poststimulus retention interval in the memory task is larger for words. This effect is most marked in the vicinity of central midline scalp. There is no such difference between word and pseudoword ERP activity in the poststimulus interval of the nonmemory control task.

(b) Maps of the scalp topography of the across-subjects averaged voltage fields for the ERP activity in Figure 5a. The maps depict the distribution of ERP activity over the scalp at the end of the delay interval (3,010–3,500 msec after stimulus offset). The difference between contour lines corresponds to a voltage increment of $.5 \mu\text{V}$. Shaded areas of the maps indicate positive amplitudes and unshaded areas indicate negative amplitudes. The maps are 90° projections with the front of the head at the top. Electrode positions are indicated by the dots. The three dots in a vertical line at the center of the map correspond (from top to bottom) to midline frontal, central, and parietal scalp sites, respectively.

Note that the word and pseudoword topographies display a marked difference over central scalp (more negativity for words) in the memory task (left column). The topographies in the control task (right column) are similar for words and pseudowords and differ from the topographies in the memory task. These results support the view that, when a conscious effort is made to hold words in short-term memory, lexical codes contribute to the maintenance process.

site (Fig. 5a, left panel). This difference was sustained throughout the delay interval, with no indication of a significant increase as the time of retrieval approached. Thus, the effect of lexicality on the ERPs reflects a process that subserves retention, rather than a retrieval-oriented process that develops during the retention interval. The effect of lexical status in the retention interval of the memory task was specific to consciously controlled memory operations; lexical status had a negligible influence on ERP activity in

the poststimulus delay interval of a “nonmemory” control task with similar attentional demands and stimulus and response processing requirements (Fig. 5a, right panel).

Lexical status and number of items to be recalled (memory load) had different effects on ERP activity during retention. Load was relatively high in the memory task (five or three items to be maintained in the delay interval) in comparison with the control task (in which only one item, either “yes” or “no,” had to be maintained in the delay in-

terval). In contrast with the effect of lexical status (largest at the midline central site), the effect of number of items to be recalled was largest at the left frontal site. Figure 5a indicates that, starting at approximately 1,000 msec after stimulus offset, the negativity over the left frontal site is largest in the word condition of the memory task (five items), next largest in the pseudoword condition of the memory task (three items), and smallest in the control task (one item).

It might be argued that greater familiarity with the phonological structures of the words in comparison with the pseudowords was responsible for the ERP results (Hulme et al. 1995). Because the words consisted of familiar combinations of familiar syllables and the pseudowords consisted of unfamiliar combinations of familiar syllables, it is possible that familiarity may have affected ease of rehearsal. However, the phonological short-term memory studies reviewed above suggest that ERP indices of phonological rehearsal effects would most likely be manifested in the amplitude of the left frontal negativity, and not at the central sites where the lexicality effect was most pronounced. The timing of the word/pseudoword topographic differences suggests that the influence of lexical status on retention begins during encoding, starting with the presentation of the second item, and continues through the delay interval. The topographic differences occurred only in the recall task, and only after presentation of the first item, so they were not likely to have been indices of the automatic activation of lexical codes postulated to occur as words are initially processed. Nor were the word/pseudoword topographic differences likely to be only the remnants of lexical processing that occurred during intentional encoding for memory, for there was no such word/pseudoword difference for the first item, and the difference was most pronounced and systematic during retention. Rather, the pattern of ERP activity suggests that the ERPs indexed the intentional maintenance of lexical codes subsequent to their activation, and that the maintenance process operated in parallel with encoding of later items in the stimulus series, then continued throughout the retention interval. Hence, the timing and topography of the ERPs in the Ruchkin et al. (1999) study support the contention that lexical processes contribute to verbal short-term memory maintenance operations when words are consciously held in working memory.

3.4. Lexical and semantic activation

Orthogonal variations of lexical and semantic properties of words to be remembered also influence brain activation during retention, with different activation patterns for lexical and semantic manipulations. Ruchkin et al. (unpublished data) presented visually to subjects a series of four different words at a rate of one word per second, followed by a 3,500 msec delay interval that terminated with a serial-recall test. All four words in a series had the same combination of levels of frequency (high or low – lexical variation) and concreteness (concrete or abstract – semantic variation).

To delineate ERP activity specific to memory operations, subjects were given a nonmemory control task in which the stimulus and postdelay interval response processing demands were similar to those in the memory task, but there was no memory requirement in the delay interval. Subjects searched the series of four words for occasional deviant tri-

als with a repeated word (probability = .10). Subjects were instructed to respond to a deviant trial with a finger movement immediately after presentation of the last word in the series, and to withhold the movement if the trial was not a deviant. At the end of the delay interval, an alphabetic character was displayed, and the subjects' task was to say the letter in the alphabet that was in the third position after the letter in the postdelay interval display (e.g., for the displayed letter "j", the response should be the letter "m"). Only nondeviant control trials were used in the ERP analyses. The same words were used in the memory and control tasks, but with different combinations of four-word series.

Error rates in the serial-recall task were 2.25% for high-frequency concrete words, 3.25% for high-frequency abstract words, 5.05% for low-frequency concrete words, and 8.16% for low-frequency abstract words. There were significant effects on error rate of word frequency ($F(1,11) = 11.65, p = .0058$) and concreteness ($F(1,11) = 8.55, p = .014$). The error rate for the alphabet search that followed the delay interval in the nonmemory control task was 1.13%. Debriefing indicated that only seven of the twelve subjects in the study employed meanings of the words in their memorization strategy.

The ERP data for all subjects ($n = 12$), regardless of memorization strategy, displayed a sustained increased negativity for low-frequency words during the delay interval, with the effect of word frequency being maximal over midline central-parietal scalp (Fig. 6, upper panel, dashed lines). No such sustained difference was found in the control task (Fig. 6, lower panel, dashed lines). The average ERP amplitude over the last 2,500 msec of the delay interval was used as a measure of ERP activity in the delay interval. ANOVA of these ERP amplitude measures at the six scalp sites in the centro-parietal midline region (C3 Cz C4 P3 Pz P4) that displayed the largest variation in sustained negativity as word frequency was manipulated revealed a significant effect of word frequency in the memory task ($F(1,11) = 11.23, p = .0065$) and no significant effect in the control task ($F(1,11) = 0.63$). Estimates of the temporal activation of the brain sources underlying the sustained increased negativity for low-frequency words indicated that the sustained increased negativity started during presentation of the third word in the series.

The ERP data for those subjects who used the meanings of the words in their memorization strategy ($n = 7$) displayed a sustained increased negativity for abstract words in the delay interval, with the effect being largest over frontal midline and left frontal-temporal scalp (Fig. 6, upper panel, solid lines). No such sustained difference was found in the delay interval of the control task (Fig. 6, lower panel, solid lines). ANOVAs of the ERP amplitude measures at the five scalp sites in the left frontal and frontal midline region (F7 F3 Fp1 Fz F4) that displayed the largest variation in sustained negativity as concreteness was manipulated revealed a significant effect of concreteness in the memory task ($F(1,6) = 10.81, p = .017$) and no significant effect in the control task ($F(1,6) = .11$). Estimates of the temporal activation of the brain sources underlying the sustained increased negativity for abstract words indicated that the sustained increase started during presentation of the second word in a series.

Concreteness also affected phasic ERP responses synchronized to the presentation of each word, with increased positivity in the ERP responses to abstract words in both

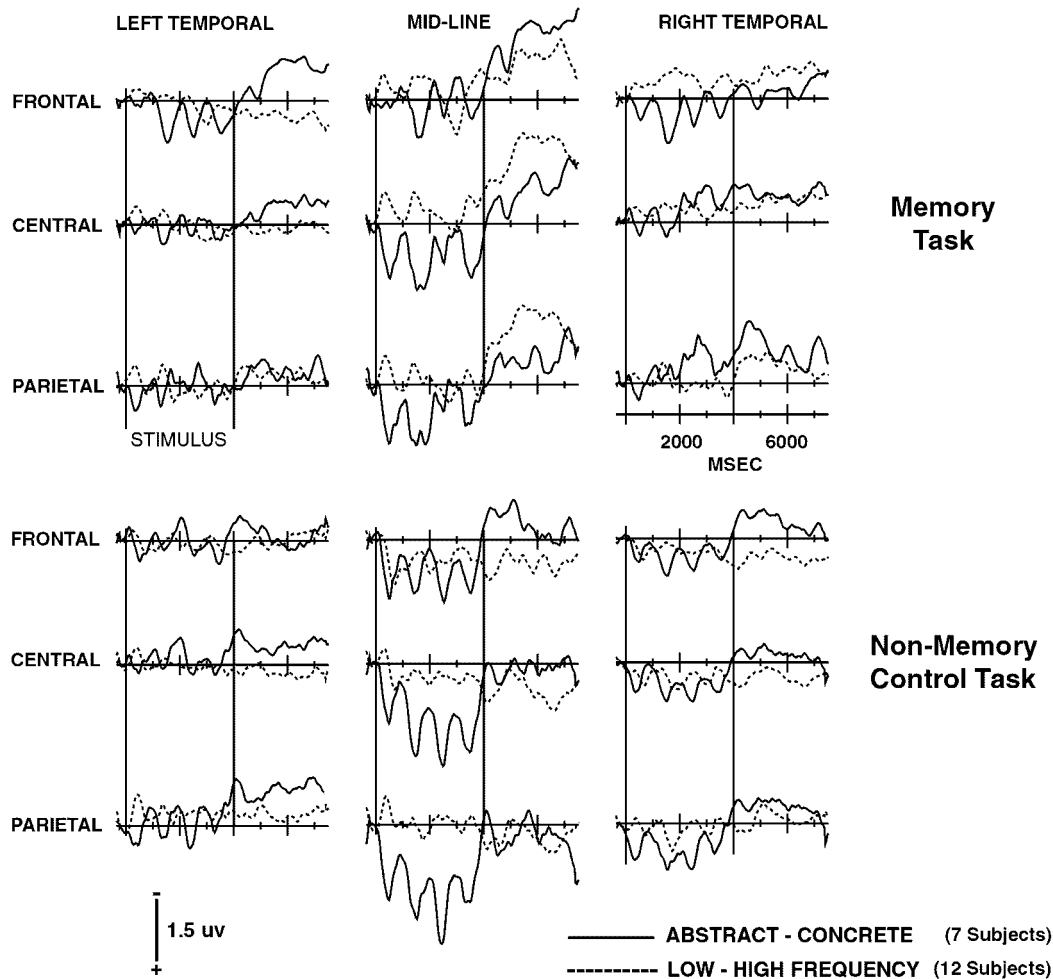


Figure 6. Across-subjects averaged scalp difference ERPs in a verbal short-term memory task (serial recall of a list of four words – upper panel) and a nonmemory control task (detect a repeated item in the list of words – lower panel). There was no memory requirement in the poststimulus delay interval of the control task. Difference ERPs show the effects of concreteness and word frequency on brain activity in the stimulus and delay intervals. The word frequency effect was revealed by subtracting ERPs elicited by lists of high-frequency words from ERPs elicited by low-frequency words (Low-High), pooled over abstract and concrete words and averaged over all subjects ($n = 12$). The concreteness effect was revealed by subtracting ERPs elicited by lists of concrete words from ERPs elicited by abstract words (Abstract-Concrete), pooled over high and low frequencies, and averaged across those subjects ($n = 7$) who employed word meaning in their memory strategy. The time axis extends from 360 msec before to 7,520 msec after stimulus onset. Stimulus duration was 4,000 msec and the duration of the subsequent delay interval was 3,520 msec. The ERPs were originally recorded with AC-coupled amplifiers (which attenuated low-frequency ERP activity). The waveforms were digitally rendered to the approximate wave shapes that would have been obtained with DC-coupled amplifiers (no attenuation of low-frequency ERP activity). The ERPs are plotted with negative polarity up with respect to a digitally linked A1 and A2 reference. The stimulus presentation interval is demarcated by vertical lines.

Note that in the memory task, during the poststimulus retention interval, the concreteness effect is largest over frontal scalp, with greater negativity for abstract words. In contrast, the frequency effect is largest over centro-posterior scalp during retention, with greater negativity for low-frequency words. In the nonmemory control task, the effects of concreteness and frequency are relatively small in the poststimulus interval. These results indicate that semantic codes also contribute to the maintenance of verbal information in short-term memory, and the combination of brain sources associated with the semantic processes differs from the combination of sources associated with the lexical processes.

the memory and control tasks. The scalp topography of these phasic responses to the stimuli differed from the sustained effect in the delay interval. In addition to the polarity difference, the phasic effect during stimulus presentation had a more posterior scalp distribution and was not lateralized to the left. For that reason it is not likely that the same brain (and therefore cognitive) processes underlie the effects of concreteness on the phasic ERP activity in the stimulus interval and the sustained ERP activity in the delay interval.

The effect of word frequency on sustained ERP activity in the delay interval is not likely to be due to pre-lexical processing such as phonological rehearsal. Other studies have reported increased sustained negativity over left frontal scalp as phonological load is increased (Ruchkin et al. 1990; 1992; 1994; 1997a). In contrast, the shift from high-frequency to low-frequency words – which caused a significant increase in error rate – resulted in an increased sustained negativity over bilateral centro-posterior scalp. The topography associated with the word frequency effect is

congruent with the effect of word versus pseudoword manipulation (see sect. 3.3; also see Ruchkin et al. 1999). However, the variation in sustained negativity when only concreteness was manipulated may be an indirect ERP sign of semantic processing during retention of verbal material because its topography is consistent with findings from short-term memory studies where phonological load or general attentional demands were manipulated (Ruchkin et al. 1990; 1992; 1994). The error rates suggest that abstract words demand greater cognitive resources in short-term memory than do concrete words. In such a case, other processing systems may have become more active as a compensatory effect when abstract words had to be retained. Nevertheless, the finding that variation of concreteness affects brain activity during the delay interval does indicate that semantic processes actively support the maintenance of verbal information in short-term memory.

3.5. Summary: Verbal working memory in serial-recall and match/mismatch tasks

Figure 7 summarizes in schematic form the timing results obtained from our ERP studies of verbal working memory in delayed serial-recall and match/mismatch paradigms. These data support the view that multiple, simultaneously active processes are involved in the short-term maintenance of verbal information (Cowan 1988; 1995; Cowan & Kail 1996). The data are consistent with the notion that phonological and lexical-semantic codes may interact throughout the retention interval, as opposed to only during retrieval. The activated lexical-semantic codes continuously counteract degradation of the material in the phonological buffer, and phonological codes may have a role in counteracting degradation of the lexical semantic codes (Martin & Romani 1994; Martin & Saffran 1997). Timing data obtained from the ERP studies indicate that the sustained lexical-semantic processes start during encoding, evidently as information concerning the properties of the material to be memorized builds up, and continue in the subsequent retention interval. Along with behavioral data (Penney 1989), the ERP time-courses also suggest that the modality-specific auditory-verbal store is more durable than the modality-specific visual-verbal store.

Timing of Activation of Verbal Short-Term Stores

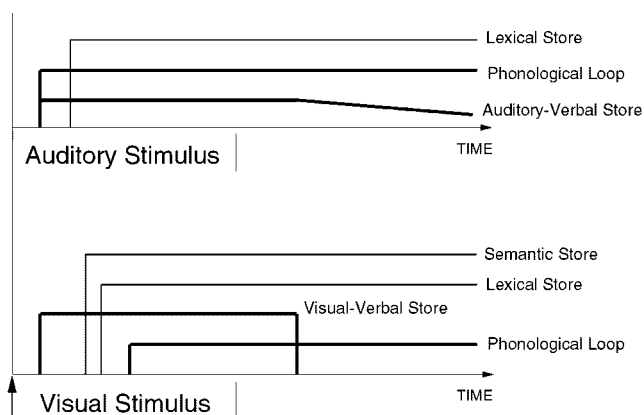


Figure 7. Schematic of the timing of hypothesized stores that contribute to the operations of verbal working memory.

3.6. Activation of long-term memory and retention

Cameron et al. (2004) used ERP responses to test the premise that retention of words in short-term memory involves activation of the words' semantic representations in long-term memory (i.e., activated long-term memory provides a representational basis for short-term maintenance of information). Cameron et al. conceptualized the instantiation of the activation process as being akin to temporally extended priming. As words are initially processed, their various representations in long-term memory are activated. The depth of processing of these words determines the levels of activation (e.g., phonological, semantic). If no conscious effort is exerted to maintain the words in working memory, then the activation of their representations decays. When a conscious effort is made to maintain the words in working memory, then the level of activation of their long-term representations remains relatively high during the retention interval.

Cameron et al.'s (2004) approach was to contrast the degree of activation in the semantic neighborhood of a series of three words used in two tasks, one that required retention of the meanings of the words and one that did not require retention of the words. The three words in the stimulus series were associated with each other. The degree of semantic activation was determined from the ERP response to an incidental probe word presented during a delay interval that followed the stimulus series. The probe word was either unrelated to the last word in the stimulus series or semantically and categorically related to the last word in the series. In effect, the three words in the stimulus series were primes and the probe word was the target for the primes. Both the series of priming words and the probe word were presented aurally. Participants were instructed that the probe word was a distractor stimulus to be ignored, and no response was to be made to it.

The degree of semantic activation was assessed by means of an ERP phenomenon elicited by the probe, referred to as N400, that is sensitive to the extent to which semantic representations of the eliciting word have been activated by the previous presentation of verbal material (Bentin et al. 1984; 1985; 1993; Holcomb 1988; Nobre & McCarthy 1994). N400 is a phasic negative deflection that is most prominent 200–800 msec after stimulus onset for auditory stimuli (Bentin et al. 1993; Holcomb & Neville 1990). N400 negativity is reduced when the eliciting word has been primed by (i.e., is in the semantic neighborhood of) previously presented verbal material and is increased when the eliciting word has not been primed (Bentin et al. 1993; Holcomb 1988; Kutas & Hillyard 1989). This variation in N400 negativity can occur even when participants are unaware of the semantic relationships (Bentin et al. 1984), and when elicited by an unattended stimulus, provided that the previously presented material was attended to (Kellenbach & Michie 1996).

Kutas and Federmeier (2000) have argued that N400 amplitude reflects the degree of difficulty with which verbal material is accessed in long-term memory. The degree of access difficulty (or ease) depends on the extent to which the verbal material is incompatible (or compatible) with the context established by previously presented verbal material. Cameron et al. (2004) reasoned that the access difficulty (or ease) would depend to some extent on the degree to which the semantic representations of previously presented

material were activated. That is, increased activation of the material's semantic representations would establish greater contextual constraints on accessing the long-term memory representations of subsequent verbal material. Hence, if maintaining the three priming words in working memory involved enhanced activation of their semantic codes, then the N400 elicited by a related probe would be smaller, and the N400 elicited by an unrelated probe would be larger, in the memory task than in the control task.

In the memory task, a set of three priming words were presented aurally at a rate of one word per second, followed by a 4,000 msec delay interval. At the end of the delay interval, a word was displayed until the participant verbally indicated whether the word matched or did not match the meaning of any of the three primes. Matches occurred in 50% of the memory task trials. An incidental probe word was presented aurally 2,000 msec after onset of the delay interval. In 50% of the trials, the probe word was semantically and categorically related to the last word of the previously presented priming set. In the other trials, the probe was neither semantically nor categorically related to any of the primes.

The control task was designed such that (1) there was no memory requirement during the 4,000 msec delay interval, (2) the depth of processing of the three priming words preceding the delay interval was comparable to that in the memory task, and (3) the operation at the end of the delay interval was comparable in difficulty to that in the memory task. To eliminate the memory requirement, there was no contingency between the operations preceding and following the delay interval. Before the delay interval, participants decided whether the priming set contained one word that

was unrelated (not associated) with the other two words. Participants were instructed to respond immediately with a vocal response if they detected an unrelated word in the priming set, and to not respond when the words in the priming set were all related. In 90% of the trials the three primes were associated (and hence there was no vocal response), and only those trials were used in the analysis of the ERP data. In control trials, the task at the end of the delay interval involved adding a visually presented pair of two-digit numbers. The display of the pair of numbers terminated when the participant responded verbally with the sum. As in the memory task, an incidental probe word was aurally presented 2,000 msec after onset of the delay interval, and was semantically and categorically related to the last word in the priming set in 50% of the trials and unrelated to any of the words in the priming set in the remaining trials.

The ERP responses to the probe for each of the four combinations of task (memory, control) and probe status (related or unrelated to the preceding three words) are presented in Figure 8. Responses elicited by unrelated probes in both memory and control tasks display enhanced N400 activity over posterior scalp compared with ERP responses elicited by related probes. Figure 9 displays the contrast between unrelated-minus-related probe difference waveforms for the memory and control tasks. Effects specific to the memory and control tasks, other than the effect of probe status, were approximately canceled in these difference waveforms. Figure 9 makes clear that the effect of semantic relatedness on N400 activity was greater in the memory task. Thus, it can be inferred from Figure 9 that retention of previously presented words results in a *gener-*

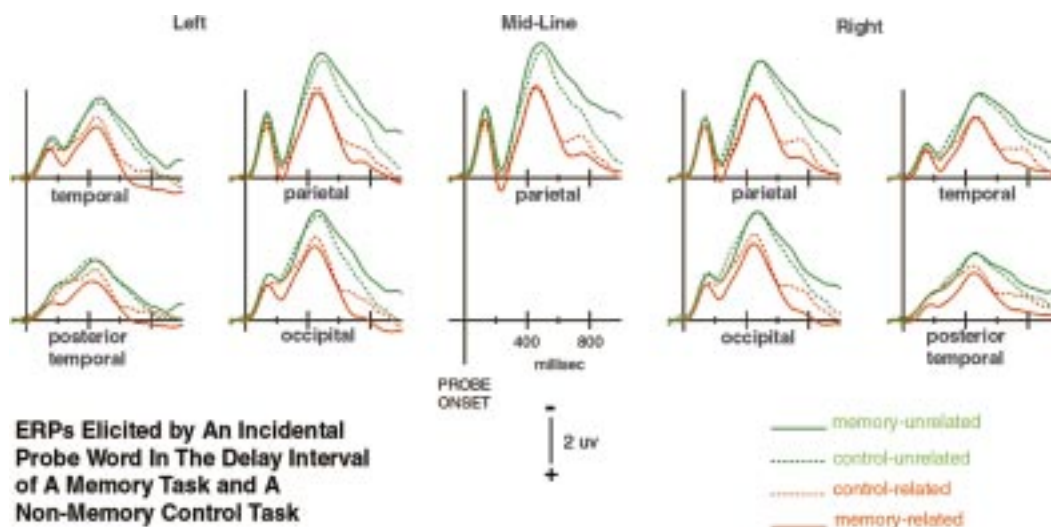


Figure 8. ERPs elicited by an incidental probe word in the delay interval of a memory task and a nonmemory control task. Shown are across-subjects ($n = 24$) averaged ERPs at posterior scalp sites, where the effects of probe status and task were largest, for the four combinations of incidental probe status and task. The vertical level of the time axis for each recording corresponds to the average amplitude in the 100-msec interval preceding probe onset. The time base extends from 100 msec prior to the incidental probe onset to 1,000 msec after probe onset. The ERPs were originally recorded with AC-coupled amplifiers (which attenuated low-frequency ERP activity). The waveforms were digitally rendered to the approximate wave shapes that would have been obtained with DC-coupled amplifiers (no attenuation of low-frequency ERP activity). The ERPs are plotted with negative polarity up with respect to a digitally linked A1 and A2 reference.

Note that the N400 activity elicited by *unrelated* probes was largest in the memory task compared to the control task, and that the N400 activity elicited by *related* probes was smallest in the memory task compared to the control task. This combination of results indicates that there was greater activation of semantic representations in the delay interval of the memory task than in the nonmemory control task.

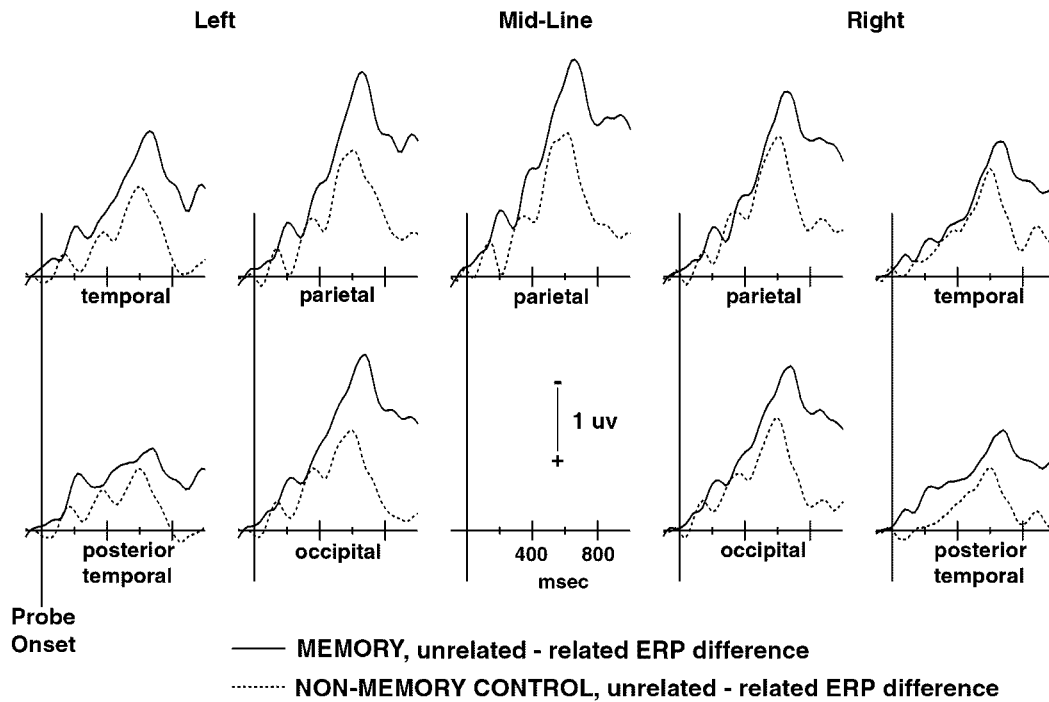


Figure 9. Across-subjects average difference ERPs for the unrelated minus related incidental probe subtraction. This figure depicts the effect of the interaction between task (memory, nonmemory control) and probe status (related, unrelated) on N400 activity elicited by the incidental probe. Note that the effect of whether the incidental probe word is semantically related or unrelated to the three priming words preceding the delay interval is greater in the memory task. The ERPs were originally recorded with AC-coupled amplifiers (which attenuated low-frequency ERP activity). The waveforms were digitally rendered to the approximate wave shapes that would have been obtained with DC-coupled amplifiers (no attenuation of low-frequency ERP activity). The ERPs are plotted with negative polarity up with respect to a digitally linked A1 and A2 reference.

ally enhanced level of semantic activation during the retention interval, as indexed by N400 amplitude and duration.

The question of whether there is *specifically* greater activation in the semantic neighborhood of words when they are maintained in short-term memory is addressed by comparing the memory and control task ERP waveforms for related probes (red waveforms in Fig. 8). Note that, for the related probes, the N400 activity in the memory task has a shorter duration and somewhat lower amplitude than in the non-memory control task. This effect is most marked at posterior temporal and occipital sites. On that ground, it can be inferred from the smaller N400s elicited by the incidental probe in the memory task that activation in the semantic neighborhood of previously presented words is greater when the words are consciously maintained in short-term memory.

These results show that retention of verbal material in short-term memory tasks that emphasize meaning is accompanied by extended, enhanced activation of the material's semantic representations. The effect of semantic relatedness on the incidental probe is not readily explained by verbal short-term memory being a separate buffer into which copies of long-term memory representations are transferred. A more parsimonious explanation is that verbal short-term memory is a process that involves continuous maintenance of long-term memory representations at enhanced levels of activation. Thus, the long-term memory representations of the related probe words may be easier to access in the memory task than in the non-memory control

task (Kutas & Federmeier 2000). Conversely, the long-term memory representations of the unrelated probe words may be more difficult to access in the memory than in the non-memory control task due to enhanced activation of non-matching features by the material held in short-term memory.

3.7. Sentence processing and semantic relatedness

The verbal working memory experiments reviewed above employed lists of unconnected items. Such paradigms have provided a useful but limited view of brain activity involved in typical verbal working memory operations. The study described here extended this view by using as the stimulus a sentence, rather than a series of unconnected words, and by requiring retention of the meaning of the sentence.

Comprehending a sentence involves a process of semantic and syntactic binding (Hagoort 2000), whereby the meanings of the words in the sentence are related to one another and maintained in short-term memory as part of an integrated overall representation. There is evidence for a postinterpretative process that maintains thematic role relations following syntactic computation on the words (Caplan & Waters 1999). This process is more error prone or engenders more brain activation, or both, when a sentence expresses more propositions (Caplan et al. 1998) – which suggests that propositions and the thematic role relations they express are maintained by a capacity-limited semantic short-term memory process. Haarmann et al. (2004) and Haarmann and Cameron (2004) sought neurophysiological

evidence for such a process by manipulating semantic relationships within a sentence and analyzing the effects of that manipulation on ERP and EEG activity in a post-sentence retention interval. The ERP results provide additional support for Crowder's (1993) proceduralist view of memory, namely, that brain systems that process particular items of information also subserve storage of those items. The EEG results provide information on the interactions among brain systems involved in the initial processing and subsequent retention of the sentence.

The short-term memory process evidently depends in part on interactions between frontal and posterior cortex implemented by the operation of frontal-posterior projection loops. The loops projecting from frontal cortex mediate the focusing of attention on representations in the posterior cortex that are to be retained, and the projections from posterior cortex provide information about the state of posterior cortical systems to frontal neural networks. Presumably the resulting influence of frontal and posterior cortical systems on each other is actualized by an increase in synchrony between neural circuits in the two brain regions. Support for this view is provided by studies of verbal and visual-spatial short-term memory tasks in which the synchronization between EEG recordings from different scalp sites was analyzed with EEG coherence measures. The patterns of coherence between EEG recordings from frontal and posterior sites were found to differ markedly between the stimulus presentation and subsequent retention intervals (Engel & Singer 2001; Sarnthein et al. 1998; von Stein & Sarnthein 2000). These findings, when combined with evidence that the same brain regions are active during both the initial processing and subsequent poststimulus retention, support the position that short-term memory operations use specific patterns of connectivity among brain regions, and not buffers that are specialized to short-term memory storage.

This position was tested by Haarmann et al. (2004) in a study of ERP activity during and following the reading of filler-gap sentences. Sentences consisting of six phrases were presented visually on a phrase-by-phrase basis over a 4,500 msec interval, followed by a 2,000 msec delay interval that ended with a probe testing the subject's memory for the meaning of the sentence. Two types of filler-gap sentences, consisting of either semantically related or unrelated nouns, were presented:

(1) What box / did the pilot / that entered / the airport / forget / in the plane?

(2) What box / did the actor / that entered / the airport / forget / in the shop?

The slashes demarcate the phrases. The underlined words indicate the nouns whose semantic relationships were manipulated. Sentence (1) contains nouns that are semantically strongly related; in sentence (2) the nouns are weak semantic associates. Semantic relatedness affected both sustained ERP activity in the post-sentence delay interval and the subjects' subsequent performance on the memory test for retention of the meaning of the sentence after the delay interval. There were more errors for sentences with unrelated nouns (11.7%) than for sentences with related nouns (7.1%). The ERP activity in the delay interval displayed sustained negativity over centro-posterior scalp. This negativity was reduced following sentences with unrelated nouns in comparison to those with related nouns. This result indicates that brain activity during retention of sen-

tence meaning is affected by semantic relationships among elements of the previously presented sentence, and is evidence for a post-sentence short-term memory process that maintains thematic role relations in linguistic discourse.

The timing of the activation of brain sources that contributed to the scalp recordings, with their approximate locations, was obtained by a brain electrical source analysis (Scherg 1990). The waveforms are displayed in Figure 10. The key finding of the source analysis was that a number of posterior cortical regions were active both on a phrase-by-phrase basis during sentence processing and subsequently on a sustained basis during the retention interval. This indicates that sentence comprehension and short-term retention of sentence meaning involve the same, or very closely located, posterior neural regions. For example, during sentence presentation, the left posterior inferior temporal gyrus displayed phasic downward deflections in response to each phrase, superimposed on a slow upward deflection that started during the second phrase and extended to the end of the sentence. The phasic responses may have reflected operations associated with encoding and syntactic and semantic processing of the individual phrases, and the slow upward deflection may have reflected integrative operations. The series of phasic responses in the left temporal lobe was followed by a relatively large sustained upward deflection during the delay interval that probably reflected retention operations. Activation in the right posterior middle temporal gyrus differed from that in the left temporal gyrus during sentence processing, consisting of somewhat lower amplitude phasic downward deflections with no slow upward deflection.

The left versus right temporal lobe differences during sentence processing may be the result of differences in the way the two hemispheres process verbal material. It has been hypothesized that the left hemisphere employs fine semantic processing and syntactic mechanisms, forming an integrated representation of sentence meaning, whereas the right hemisphere employs coarse semantic processing and word-by-word operations that support, but do not supplant, left hemisphere processing (Beeman 1998; Faust & Chiarello 1998; Kircher et al. 2001). During the delay interval, however, when the meaning of the complete sentence was available, activation in the right temporal lobe also consisted of a sustained upward deflection, probably reflecting retention of the overall meaning of the sentence (Kircher et al. 2001). The timing of activation in the temporal lobes (and also the left posterior parietal gyrus) is evidence that brain regions that contribute to sentence processing, indicated by activation synchronized with phrase-presentation, also contribute to subsequent retention operations, as indicated by sustained activation in the delay interval.

Transient activation in the left lingual gyrus began during the first phrase of the sentence and gradually diminished during the subsequent retention interval. The transient activation in the lingual gyrus contributed positive polarity activity to the scalp ERP recordings, and may be an instance of the operation of a specialized visual-verbal buffer supporting reading via activation of visual codes, as found in the Ruchkin et al. (1997a) study reviewed above, which contrasted ERPs elicited by verbal material that was either read or heard. Right prefrontal cortex displayed phasic activity in response to the first two phrases of the sentence; sustained activation began during the third phrase of the sentence. Sustained activation in the left insula did not

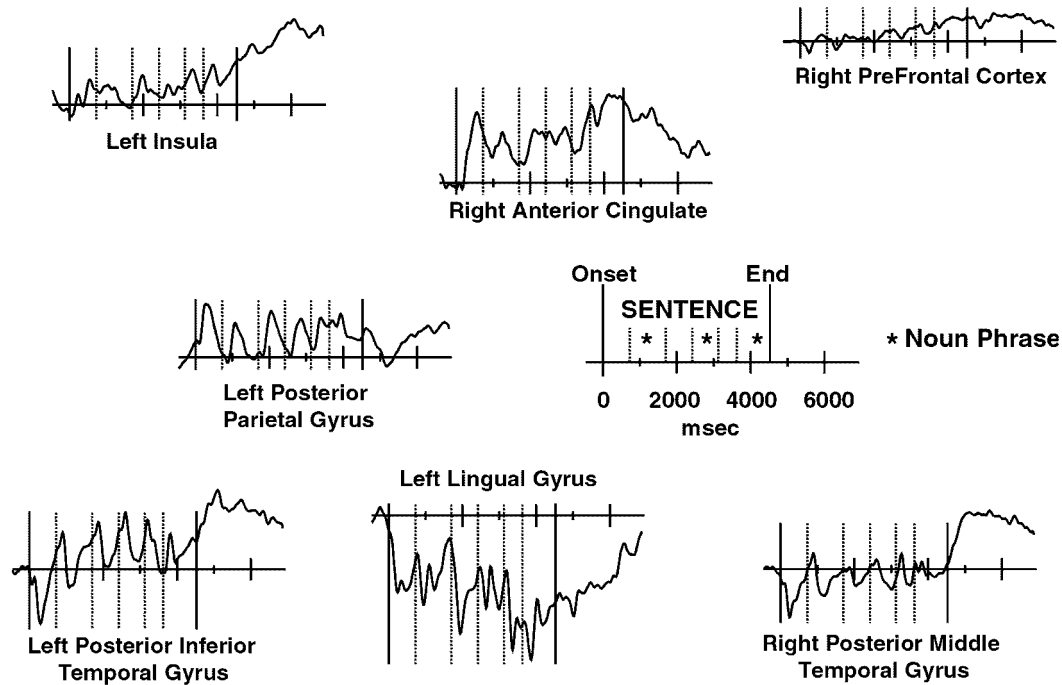
BRAIN ACTIVATION DURING THE COMPREHENSION AND RETENTION OF SENTENCES

Figure 10. Estimated time courses of cortical activation during comprehension and retention of the meaning of filler-gap sentences with unrelated nouns. The time axis extends from 460 msec before to 6,960 msec after sentence onset. The sentences were presented visually, phrase-by-phrase (the phrase durations are demarcated by the vertical dashed lines). The waveforms and their brain locations were estimated from a source analysis (Scherg 1990) of across-subjects ($n = 16$) averaged scalp ERPs recorded from a 24-channel montage. The vertical scale is in arbitrary units. Upward deflections indicate negative polarity contributions to the scalp recorded ERPs, and downward deflections indicate positive polarity contributions. The ERPs were originally recorded with AC-coupled amplifiers (which attenuated low-frequency ERP activity). The waveforms were digitally rendered to the approximate wave shapes that would have been obtained with DC-coupled amplifiers (no attenuation of low-frequency ERP activity).

Note the marked responses to the presentation of each phrase during sentence comprehension, followed by sustained activation during the postsentence retention interval in the left posterior parietal gyrus, and the left and right temporal lobes. This timing pattern indicates that these brain regions were active both during processing and subsequent retention of the sentences.

begin until the last phrase of the sentence, when stimulus delivery was nearly complete, suggesting that the left frontal control mechanisms supporting retention do not become fully operative until meaning has been established.

3.8. Summary: Brain mechanisms of verbal working memory

The Cameron et al. (2004) and Haarmann et al. (2004) ERP studies reviewed above buttress models of memory in which the long-term stores for items of information are located in the same brain regions that are involved in the initial encoding and processing of the items, and also support the hypothesis that short-term memory maintenance of the items consists of reactivation of the long-term memory representations. Further support for the view that the same brain regions underlie perception, storage, and reactivation of information is provided by a recent fMRI study by Wheeler et al. (2000), who found that, during vivid recollection of auditory and visual material, there is increased fMRI activity in a subset of the brain regions that previously displayed increased fMRI activity during perception of the material.

4. Synchronization between brain systems

4.1. EEG coherence, background

The timing of the ERPs indicates that different brain systems operate in parallel during encoding and retention operations. Coherence analysis examines the degree to which such parallel processes are synchronized, addressing the issue of interactions and binding among brain systems. Intracranial studies of neural activity in animals engaged in perceptual processing have shown that the activity of neurons that process different aspects of a stimulus becomes synchronized (Engel & Singer 2001), indicating that neural synchronization is a part of the process that binds together disparate features of a percept.

Neural synchrony in humans has been investigated by using the coherence of EEG brain rhythms¹ recorded from different scalp locations (Varela et al. 2001). As examples, Rodriguez et al. (1999) recorded multichannel EEG activity when subjects viewed ambiguous stimuli that could be perceived as either faces or meaningless objects. They found enhanced EEG synchronization between frontal and occipital recording sites only when the stimuli were perceived as faces. Weiss and Rappelsberger (1998) found that

EEG coherence was sensitive to semantic properties of linguistic stimuli. Von Stein et al. (1999) analyzed EEG activity during presentation of objects in either pictorial, spoken, or written modes. They did not find any region whose activation was specific to word processing (i.e., the same increase in activation for both auditory and visual presentation of words). Rather, what was common to the auditory and visual processing of words was increased synchronization between temporal and parietal cortex.

Marked differences have been found between coherence patterns in encoding and retention intervals of short-term memory tasks, with the character of the differences evidently depending on the task demands. Sarnthein et al. (1998) investigated EEG coherence during retention of verbalizable character strings or abstract line drawings. They compared coherence during retention with (1) coherence during stimulus presentation and (2) coherence in a control condition with no memory requirement, and found that coherence between anterior and posterior sites was greater during retention in the 4–7 Hz band. For verbal material, bilateral frontal/prefrontal sites displayed increased synchrony with left posterior sites during retention. For visual material, there was increased synchrony between frontal/prefrontal sites and bilateral posterior sites during retention. Apparently, increased synchrony between frontal control regions and posterior perceptual processing regions is a component of the neural processes underlying maintenance of information in working memory.

4.2. Sentence processing and retention: Coherence analysis

In addition to the analysis of ERP activity during sentence processing and retention, Haarmann et al. (2002) examined how coherence patterns vary as a function of both the mode of mental operation (sentence comprehension versus retention of sentence meaning) and the semantic characteristics of the sentence (sentences with either related or unrelated nouns). To reduce the influence of volume conduction on the coherence measures, coherences were computed from current source densities derived from the EEG (Nunez et al. 1999; Srinivasan et al. 1998).

Coherences were lowest in a no-task baseline condition preceding presentation of the sentences, consistent with the result of the Sarnthein et al. (1998) comparison of retention with a no-memory control task. However, comparison of coherences obtained during the processing and subsequent retention of sentences in a Haarmann and Cameron (2004) study produced a pattern of coherence variation across conditions that differed from what Sarnthein et al. (1998) found in their comparison of coherences obtained during presentation and retention of a series of words. Haarmann and Cameron found that coherences in the 4–6 Hz band were generally larger during sentence processing than during retention (Fig. 11, top row). During sentence processing the pattern of coherences was characterized by “local” connections over posterior scalp (bilateral occipital-temporal and left occipital-parietal pairs) and was “long range” within and across hemisphere connections between the left anterior temporal site (E2) and both frontal and posterior sites. In contrast with coherences in the 4–6 Hz band, coherences in the 10–14 Hz band were larger during retention than during sentence processing, with the enhanced 10–14 Hz coherence occurring bilaterally (Fig.

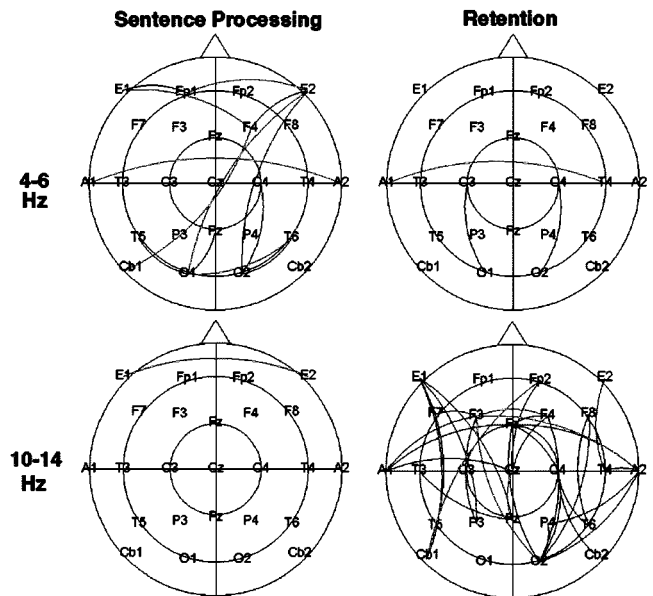


Figure 11. Comparison of coherences during sentence processing and retention, indicating those electrode pairs for which the coherence during processing of sentences with unrelated nouns (left column), or during the subsequent retention of the sentences (right column), were reliably larger than during the presence baseline interval. The lines connecting electrode pairs indicate those pairs for which the coherence was greater by 20% or more, than the pair's presence baseline level with a statistical significance level of $p < .01$. The panels in the column to the left display the electrode pairs with the requisite coherence during the last 1,500 msec of sentence processing. The panels in the column to the right display the electrode pairs with the requisite coherence during the last 1,500 msec of the retention interval following the sentence. Coherences meeting the above criteria were found in the 4–6 Hz band (top row) and 10–14 Hz band (bottom row).

Note that in the 4–6 Hz band there are more electrode pairs displaying increased coherence (relative to the pair's presence baseline level) during sentence processing than during retention of the meaning of the sentence. In contrast, in the 10–14 Hz band there are far more electrode pairs displaying increased coherence (relative to the pair's presence baseline level) during retention than during sentence processing.

11, bottom row). The 10–14 Hz coherences in the retention interval were mainly between frontal-posterior pairs of electrode sites. Within the retention interval, coherences in the 10–14 Hz band were generally larger following sentences with semantically unrelated nouns in comparison to those with semantically related nouns.

These results indicate qualitatively different patterns of synchrony among brain regions as a function of mode of operation (sentence comprehension versus retention of sentence meaning) and type of material maintained in short-term memory (meanings of sentences with semantically related or unrelated nouns). The synchrony is a reflection of the production of cotemporal activation that, in the retention mode, serves to reinforce the maintenance of codes within activated areas.

5. Conclusion

The results of the ERP, EEG coherence, and hemodynamic studies discussed above lead to the conclusions that (1) re-

tention of information in working memory entails sustained activation in posterior brain systems whose functions are in the domain of perception (e.g., Fig. 2) or which participate in the initial determination of the meaning of the information (e.g., Fig. 10), or both; and (2) the divergence between initial processing and subsequent retention operations lies, in part, in the way in which the posterior processors interact with frontal systems (e.g., Fig. 11). During retention, processing shifts away from an input-driven bottom-up mode to a top-down mode. In this view, there is no reason to posit specialized neural systems whose functions are limited to those of short-term storage buffers and are distinct from long-term memory systems, as proposed by Baddeley (2001a). Rather, activated long-term memory stores associated with the posterior processing systems are the likely neural substrate for short-term retention of the types of information contained in our tasks. Long-term memory systems in posterior cortex are initially activated for the processing of incoming information (e.g., percept formation, comprehension). Subsequent interactions with other cortical systems sustain activation of the posterior long-term memory networks, thereby enforcing temporary retention of the information.

Our view is that the influence on posterior cortical systems of control processes mediated by prefrontal cortex is the principal *mechanism* for conscious maintenance of certain forms of information in working memory. We view the findings of attention-based maintenance for visuo-spatial material (Awh et al. 2000; Awh & Jonides 2001) and enhanced semantic activation for verbal material during retention (Cameron et al. 2003) as different aspects of this mechanism. The results from Awh and colleagues emphasize the attentional control aspect and those from Cameron and colleagues emphasize the sustained activation of long-term memories. In other words, visuo-spatial and verbal short-term retention systems use the same underlying mechanisms. As stimuli are perceived and processed in posterior cortex, long-term memory codes are activated. Which representations become activated depends on the subject's prior experience relevant to the stimulus. In the case of verbal stimuli, activated codes could include phonological, lexical, and semantic representations. If a stimulus consists of familiar words whose meanings are well understood, then phonological, lexical, and semantic codes all may be activated. If the stimulus consists of novel words, then primarily phonological codes would be available from prior experience for processing the unfamiliar material. Thus phonological rehearsal usually plays a critical role in language acquisition (Baddeley et al. 1998; Gathercole & Baddeley 1989; 1990; 1993; Gathercole et al. 1997).

In the above construct, neural systems in frontal cortex are responsible for attentional control operations. Although not addressed by our experiments, the frontal cortex also has its own long-term stores of representations (e.g., themes, schemas, etc.). These stores are distinct from those of posterior cortex.

The systems of neural connections that specify the combinations of elemental stimuli constituting long-term episodic memories become activated with the occurrence of familiar events. For novel episodic information, the neural systems that ultimately become the repositories of the consolidated long-term episodic memory for the novel information are initially active, with the hippocampus providing coordinating control. In this view, short-term epi-

sodic memory consists of well-consolidated and partially consolidated long-term episodic memories in an active state.

Unless a conscious effort is exerted, activation of the percepts and products of information processing will decay, with the rates of decay depending on the type of information and subsequent processing demands (e.g., a new trial or interfering conditions). Sustained activation of a memory trace is mediated largely by prefrontal cortex interacting with posterior cortical systems. In the case of verbal material, operation of the phonological rehearsal may augment sustained activation of phonological codes, although rehearsal may not always be necessary (see Richardson et al. 1996, on the extended persistence of the phonological trace when rehearsal is suppressed).

This view of memory does not call for separate, distinct neural systems for short-term storage of information. The initial processing of a stimulus involves the activation of long-term memory codes. Sustained activation of the long-term memory codes can produce results that give the appearance of the operation of a separate short-term buffer with fast-acting weights, but how would these anatomically, functionally distinct short-term storage systems be organized and how would they operate in neural terms? How would a separate visual short-term store have the ability to represent the great variety of visual experiences without replicating the anatomical-functional specificity of the perceptual facilities of the visual cortices? How would a phonological short-term buffer represent the various possible phonological properties of verbal stimuli without duplicating the anatomical-functional specificity of the cortical circuitry that initially implements phonological processing?

We take the parsimonious view that the long-term memory systems associated with the posterior cortical processors provide the necessary information representation basis for short-term memory, with the property of short-term memory decay being due primarily to the posterior system. Prefrontal cortex provides the pointer system for maintaining activation in the appropriate posterior processing systems. We assume that the "number of pointers" is limited (i.e., the amount of information that can be in the focus of attention is limited). Consequently, due to the pointer limitation, we attribute properties such as short-term memory capacity and displacement of information in short-term memory mostly to the functioning of the prefrontal system. To put it succinctly, short-term (or working) memory is a process based on the activation of long-term memory structures.

NOTE

1. The coherence function provides a measure of the degree of correlation between a pair of signals as a function of frequency. For EEGs, the signals are recordings from a pair of electrode sites. The coherence between a pair of signals at a given frequency is approximately equivalent to (i) filtering each signal with a very narrowband filter with a passband centered about the given frequency, and (ii) then computing the squared correlation coefficient of the filtered signals. The amplitude of a coherence function can range from a minimum of zero to a maximum of +1.0. Coherence functions are useful in the study of neural signals and cognitive behavior because systematic relationships have been found between mental states and the frequency composition of concomitant neuroelectric activity (Klimesch 1999). For a concise, cogent review of the application of coherence functions to EEGs, see von Stein and Sarnthein (2000).

Coherence values can be statistically analyzed with the same

types of designs as employed for ERP amplitudes and behavioral variables. However, because the probability distribution of coherence values is very different from a Gaussian probability distribution, it is best to use nonparametric tests for evaluating the statistical significance of experimental effects.

APPENDIX

ERP SCALP TOPOGRAPHY AND BRAIN SOURCES

The scalp distribution of ERP activity can be used to make inferences about the brain sources of scalp-recorded ERP data. ERP scalp distribution at a given instant in time is commonly visualized by plotting topographic maps of the ERP voltage amplitudes or current source densities (CSDs) on the surface of the scalp. CSDs can be derived from the ERP voltage amplitudes. The derivation process can be thought of as a high-pass spatial filter that reveals those scalp regions where current inflow or outflow is greatest. In comparison with voltage maps, CSD maps generally provide more sharply defined topographic features. CSDs are sensitive primarily to activity generated near the surface of cortex; voltage maps provide a better reflection of activity generated in deeper brain regions. When the shapes of the topographic maps differ between conditions (or latencies), it can be concluded that different combinations of brain sources are active in the different conditions (or latencies).

Spatiotemporal analysis, which uses scalp distributions at all time points of the ERP activity, can be used to make inferences about the locations and timing of brain sources that contribute to the scalp recordings (Scherg 1990). Estimating locations of the brain sources from scalp-recorded ERPs involves solving an inverse problem with no unique solution. Hence, the estimated locations and time courses of activity of the sources can only be approximate. The inverse problem can be constrained somewhat by employing relevant ancillary neurophysiological and anatomical information. A commonly used commercial implementation of spatiotemporal analysis, Brain Electric Source Analysis (BESA 2000, v4.2), was used in the studies reviewed in this article. Miltner et al. (1994) conducted a simulation study of BESA, and found an average error of 1.4 cm for source location in a spherical head model with a 17-cm diameter. The correlation coefficient between the actual and estimated wave shapes of the sources' activation was 0.89. Miltner et al. concluded that estimates of the wave shapes of brain source activity are more robust than estimates of source location, in the sense that location errors do not have a marked effect on the wave shapes, which generally bear a reasonably close resemblance to the wave shapes of the actual sources.

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Open Peer Commentary

Attention-based maintenance of speech forms in memory: The case of verbal transformations

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Abstract: One of the fundamental questions raised by Ruchkin, Grafman, Cameron, and Berndt's (Ruchkin et al.'s) interpretation of no distinct specialized neural networks for short-term storage buffers and long-term memory systems, is that of the link between perception and memory processes. In this framework, we take the opportunity in this commentary to discuss a specific working memory task involving percept formation, temporary retention, auditory imagery, and the attention-based maintenance of information, that is, the verbal transformation effect.

In a recent study (Sato et al. 2003), we used functional magnetic resonance imaging (fMRI) to localize the brain areas involved in a specific verbal imagery task: the Verbal Transformation Effect (VTE, Warren & Gregory 1958). This effect, which is analogous to the perceptual rivalry in ambiguous figures in the visual domain, relies on the fact that certain speech sequences, when repeated over and over, yield a soundstream which allows more than one segmentation. These can appear during production, that is, when subjects repeatedly utter the stimuli either overtly or covertly (Reisberg et al. 1989; Smith et al. 1995), and also during perception, that is, when subjects listen to an auditory speech stimulus looped on a tape (Warren 1961). In our fMRI study, two conditions were contrasted: one involving simple mental repetition of phonological items (baseline condition) and the other involving mental repetition of the same items with active search for verbal transformation (VTE condition). The verbal transformation task was associated with a left-lateralized network of frontal-parietal areas similar to those classically involved in verbal working memory¹ (Cohen et al. 1997; Honey et al. 2000; Paulesu et al. 1993), specifically, the inferior frontal gyrus (IFG) and insular region, supramarginal gyrus (SMG), premotor and supplementary motor areas, dorsolateral prefrontal cortex, and cerebellum.

Given that the VTE task engaged very little demand on verbal storage, the hypothesis of the inferior parietal cortex's involvement (e.g., Paulesu et al. 1993) in short-term storage of phonologically coded verbal material must be examined. Hickok and Poeppel (2000) offer a hypothesis that can better account for our results. According to them, the SMG would not be the storage site for storage of phonemic representations per se, but rather serves to interface sound-based representations of speech in the auditory cortex with articulatory-based representations in the frontal cortex via sensorimotor recoding. We suggest that a frontal-parietal circuit is utilized in the VTE, in which the SMG would be involved in the construction of phonological representations, by activation of long-term memory representations of the "speech body," that is, the vocal tract. Moreover, the classical view of production in the literature on verbal working memory, that the inferior frontal gyrus (specifically Broca's area) is directly implicated in subvocal rehearsal, deserves to be revised.

Considering, on the one hand, that our VTE activations come from a subtraction of the baseline (involving subvocal rehearsal itself) and, on the other hand, that the IFG is activated during the

VTE task, it seems indeed difficult to exclusively assign a purely rehearsal role to this region. In accordance with this, the classical view of Broca's area as a major structure for speech production has been re-evaluated by Murphy et al. (1997), who found no activation of the IFG during automatic speech tasks, either overtly or covertly. Then, building on different studies that have demonstrated the implication of the IFG in phonological tasks (e.g., Pol-drack et al. 1999) and in the observation and mental imagery of actions (Buccino et al. 2001), we hypothesize that the role of the IFG is that of an attentional matching system for action understanding, which is well adapted to a linguistic processing such as syllable parsing during the VTE.

In summary, these results are strongly consistent with the authors' view of working memory entailing, in one part, activation in posterior brain systems for percept formation and meaning determination and, in the other part, processing shifts away from posterior input-driven mental states to a frontal top-down mode for conscious and attentional maintenance of information during the retention phase. Furthermore, because the VTE provides some language equivalent of the ambiguous image paradigm in vision, it could lead to brainweb asymmetries similar to those displayed by Rodriguez et al. (1999) and mentioned in the target paper. For example, the preference in the VTE for words over nonwords (Pitt & Shoaf 2002) could be a result of a learning-based larger synchronization pattern, just as the preference for a meaningful visual stimulus over a meaningless one. In this context, it is not without interest to notice that the perceptuo-motor loop involved in the (mental repetition + transformation search) task we used in our study, could induce some intrinsic synchrony resulting from enaction per se. Indeed, in a complementary study (Sato & Schwartz 2003), we raised the assumption that in a sequence of sounds like [laIflaIflaIflaI] (repeating "life" over and over), the articulatory speech production system would naturally synchronize the production of the fricative "f," the liquid "l," and the diphthong "I" into a group [flaI], while in the sequence [laIf] the "l" in onset and the "f" in coda are naturally desynchronized. Hence, we expressed the prediction that "life" should be more often transformed into "fly" than the other way round. This is indeed the kind of pattern we found, both in overt and covert repetition, in an equivalent contrast in French. In this paradigm, it is likely that phase transitions in dynamical systems possibly involved in the speech production process (Tuller & Kelso 1990) would enhance the potential synchrony of one pattern over the other one, both at the stimulus production level, and at the brain wave level.

In conclusion, the verbal transformation effect seems to provide a nice pivotal point between perception, decision, attention, imagery, and memory, to test some of the ideas quite convincingly expressed by the authors of the present target paper.

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NOTE

1. This result of the use of verbal working memory during verbal imagery is also consistent with previous studies of imagining speech by McGuire et al. (1996) and Shergill et al. (2001).

New data: Old pitfalls

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Abstract: Ruchkin et al.'s theoretical conclusions reflect two venerable fallacies. They confound an experimental paradigm with a theoretical concept, and they assume that features of the paradigm that are most readily detected by their methods provide an adequate account of the operation of the theoretical system. This results in a simplistic theory that does not do justice to the richness of the available data.

Some forty years ago, Melton (1963) published a classic paper in which he argued that the concept of short-term memory (STM) was unnecessary, because all available data could be explained in terms of long-term memory (LTM) processes. His paper performed two important services: the first was to present a convincing case for the position that many STM paradigms shared characteristics with LTM; the second was to demonstrate two pitfalls – by falling into them. The first, the nominalist fallacy, assumes that if a paradigm and a theoretical concept are given the same name, then all characteristics of that paradigm can be attributed to the concept. The second, the correlationist fallacy, is to further assume that any variable that is broadly correlated with performance on the paradigm is crucial to it. These shortcomings were pointed out by Waugh and Norman (1965), leading to their distinction between STM, a paradigm label, and primary memory, a theoretical construct, and to the parallel distinction made by Atkinson and Shiffrin (1968) between STM, a paradigm, and STS, a hypothetical store. Ruchkin et al. appear to be intent on repeating Melton's mistakes, although they refer to their nominal system as working memory (WM), and base their argument primarily on electrophysiological data.

Ruchkin et al. report a range of STM studies primarily focusing on electrophysiological activity occurring between the offset of stimulus presentation and subsequent delayed recall. In short, they focus on maintenance rehearsal, an important but not essential feature of the STM paradigm, and even less central to the much broader concept of WM.

Like Melton, they find similarities between data from STM and LTM paradigms, in their case, patterns of activation, which they assert are highly similar. This, they argue, differentiates their theory from the Baddeley and Hitch WM model, which they seem to assume postulates no role for LTM in the operation of WM. We do indeed reject the generalization that WM is activated LTM, not because of denying the role of LTM, but because such a view offers a simplistic answer to a complex question. LTM influences WM in a range of different ways that go beyond the concept of simple activation (Baddeley 2000; 2002).

Consider, for example, the phonological loop, perhaps the simplest component of WM. Baddeley (2002) assumes a role for LTM operating in at least three different ways. The first of these is reflected in the recency effect, which we suggest involves an active WM strategy applied to a passive priming process (Baddeley & Hitch 1993). Such priming may occur within any of a wide range of representations, from brief post-perceptual stores to long-term episodic, autobiographical, or semantic memory representations.

The second contribution of LTM concerns the role of implicit learning. Consider, for example, the immediate recall of letter sequences. Those that resemble the phonotactic structure of the rememberer's native language are consistently better retained over a brief interval than are less word-like sequences (Gathercole 1995). Although this is a powerful effect for recall, it is virtually absent when performance is tested by recognition (Gathercole et al. 2001), a result that can readily be fitted into the phonological loop model by assuming that the store itself is relatively immune to language habits, whereas the rehearsal mechanism is very language-sensitive (Baddeley 2001a). LTM is clearly important, but in a way that is richer and more complex than simple activation.

A third level at which LTM might influence utilization of the phonological loop concerns the application of conscious strategy. For example, participants tested on immediate memory for word sequences typically ensure that all their responses are real words, and are taken from the appropriate set. This process presumably depends on executive control of both semantic memory and episodic LTM. Simply detecting activity in some or all of the brain regions thought to underpin such LTM storage and control systems, however, adds little to our understanding.

This relates to my second concern, the correlational fallacy; this assumes that activity that clearly coincides with an STM paradigm must be responsible for the behaviour observed. Figure 4a in Ruchkin et al., for instance, shows one of the clearest of the elec-

trophysiological differences reported, namely that between retention of visually and verbally presented items. As Penney's (1989) review indicates, modality effects do occur in STM. Under most conditions, however, their magnitude is quite small and largely limited to an increased recency effect (Conrad & Hull 1968; Laughery & Pinkus 1966; Murdock 1972); this contrasts with phonological coding, which has a substantial and pervasive influence on verbal STM regardless of whether input is visual or auditory (Baddeley 1966a; Wilson 2001). It therefore seems likely that Ruchkin et al.'s interpretation of their modality effect reflects the correlational fallacy, being readily detected by ERP techniques, but having only a limited impact on memory performance.

Finally, Ruchkin et al. make much of the differences between my own approach and that of Cowan. In fact, our genuine differences are really quite small (Baddeley 2001b; Cowan et al. 2003). We both agree that activated LTM plays an important role in WM, but to do so requires the maintenance and manipulation of some kind of representation. I postulate the episodic buffer as a possible mechanism, whereas Cowan refers to holding "pointers" to activated LTM. To me, this seems too passive a concept to capture the creative manipulation capacity, which in my view, allows WM to serve as a workspace capable of both representing the past and planning for future action.

Working memory is a complex multifaceted system. By using a combination of techniques from cognitive psychology, neuropsychology, and neuroimaging, we have made progress in teasing apart its varied components. Electrophysiological methods offer a valuable additional tool, particularly for analyzing active processes such as maintenance rehearsal. Despite their technological sophistication, however, electrophysiological techniques, like other existing methods, provide a useful, but still rather blunt, instrument. For that reason, it is important to use them wisely, in combination with other methods, and with due regard to the theoretical pitfalls that have ensnared us in the past.

Tidying up sensory stores with supraordinate representations

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Abstract: In attempting to integrate the authors' proposed model with results from analogous human event-related potential (ERP) research, we found difficulties with: (1) its apparent disregard for supraordinate representations at posterior multimodal association cortices, (2) its failure to address contextual task effects, and (3) its strict architectural dichotomy between memory storage and control functions.

In support of their proposal, Ruchkin et al. rely mostly on human event-related potential (ERP) research with delayed matched-to-sample (DMS) task paradigms. In particular, scalp distributions of modality-specific ERP waves measured during the retention S1-S2 interval of DMS tasks are taken to support a common anatomical substrate of short-term (STM) and long-term memory (LTM) representations. In order to become a truly parsimonious – rather than an overly simplistic – explanation of working-memory retention mechanisms, the proposed model should be able to account for ERP results from other paradigms also involving short-term retention of information. Here we attempt to integrate the authors' views with recent ERP results from selective attention (Barceló et al. 2000a) and task-switching paradigms (Barceló et al. 2000b; 2002). Although our ERP results are partly consistent with the authors' proposal, we found difficulties with: (1) their relative disregard for supraordinate memory representations at posterior multimodal association cortices; (2) their failure to address con-

textual (i.e., prestimulus) task effects; and (3) their strict architectural dichotomy between memory storage and control functions.

There are some straightforward similarities between DMS and selective attention tasks. In a DMS task, memory representations for S1 need to be retained on-line for the 3 to 10 sec duration of a S1-S2 interval. Instead, in selective attention tasks, memory representations for target stimuli are to be retained for 3 to 10 min, the typical duration of a block of trials. In these tasks, the memory representations for target stimuli are called "attentional templates," as they are to be matched with all incoming stimulation for target selection. In line with the authors' proposal, this template-matching process involves prefrontal activation of modality-specific cortical regions devoted to the analysis and long-term storage of stimulus features. This process, however, can be further fractionated into a sequence of stages, each reflecting distinct interactions between higher- and lower-ordered memory representations leading to object identification. For example, both tonic and phasic top-down modulations contribute to the early analysis of target features (e.g., visual P1; Barceló et al. 2000b), although not all such modulations depend exclusively on prefrontal cortex (e.g., visual N1 to standards; Barceló et al. 2000b). Importantly, there is concurrent phasic activation of prefrontal and posterior multimodal association cortices after target identification (e.g., N2, P3b components; Barceló et al. 2000b). It is not clear how this multimodal posterior ERP activation may lend support to the authors' proposal.

Like DMS tasks, task-switching (TS) paradigms also require on-line maintenance of task-relevant information during a variable S1-S2 time interval. Yet these two task paradigms differ substantially in the level of abstract memory representations involved. For example, in a visuospatial DMS task, subjects need to apply just one fixed task-rule throughout (i.e., "if S1 equals S2, then y, else z"; where S1, S2 are exemplars of a given semantic or perceptual category, e.g., line orientation; whereas y and z designate different motor programs, e.g., go/no-go responses). In contrast, the S1 stimulus in a TS paradigm prompts subjects to update, maintain, and transform information about the current task rules (also, task set, attentional set, or task context), hence involving a higher class of supraordinate memory representations (i.e., "if S1 equals <shift>, then rule 2, else rule 1"; where rule 1, rule 2 denote two different task sets; i.e., rule 1 = "if S2 equals <vertical line> then y, else z"). In accord with the authors' proposal, one would expect enhanced neural activation at modality-specific cortical areas devoted to the sensory analysis of S1 features. On the contrary, in our TS paradigm we found enhanced ERP activation across a multimodal fronto-parietal network in response to S1 stimuli (e.g., involving both P3a and P3b responses; Barceló et al. 2002). Admittedly, a shift S1 cue prompts for both the updating and reconfiguration – not mere retention – of contextual task information in working memory. In addition, memory retention and consolidation of individual task rules can be examined over a series of nonshift trials. A gradual post-shift build-up in the amplitude of endogenous ERP responses to target S2 stimuli was observed across nonshift trials. Such a steady enhancement mostly affected the target P3b response, and was attributed to a gradual strengthening and consolidation in memory of the recently established task-rule. These results from TS paradigms emphasize the importance of context-dependent supraordinate memory representations (i.e., task-rules) in accounting for target-related ERP effects in working memory tasks (Barceló et al. 2000b; 2002).

With their emphasis on modality-specific ERP effects from DMS tasks, Ruchkin et al. might overlook the relative importance of multimodal memory representations in a variety of working-memory processes. For example, it has been proposed that clusters of multimodal rule-coding neurons in prefrontal cortex may combine subsets of feature-coding neurons to allow for rapid shifts of activation across entire sets of posteriorly-distributed sensory memory representations (Dehaene & Changeux 1995). In general, such a type of multimodal memory representation is con-

sistent with the well-established nature of conceptual representations in STM (Sachs 1967; 1974) and LTM (Craik & Tulving 1975) linguistic processing.

Finally, the proposed model seems to implicitly assume at least one of Baddeley's (2001a) central tenets, that is, a strict architectural separation between posterior memory retention and anterior control systems. In so doing, the model seems noncommittal about the critical operations of shifting, updating, and reconfiguring of task-relevant information in working memory. Instead, the ERP evidence reviewed here suggests a less strict anatomical distinction between storage and control functions (Barceló et al. 2000b; 2002). As a plausible alternative to this dichotomy, a context processing model has been proposed as a simple representational mechanism capable of subserving both memory storage and control operations through the functional integration of activities from prefrontal and posterior association cortices (Braver et al. 2002). From a cognitive neuroscience perspective, a valid model of working-memory function should provide an integration of evidence across a wide range of task paradigms at the crossroads of a variety of higher cognitive functions (i.e., Fuster 2003).

Varieties of procedural accounts of working memory retention systems

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Abstract: The present commentary agrees with many of the points made by Ruchkin et al., but brings up several important differences in assumptions. These assumptions have to do with the nature of the capacity limit in working memory and the possible bases of working-memory activation.

I find much to like about Ruchkin et al.'s target article. The authors agree with my theoretical conception of working memory (Cowan 1995; 1999) and provide more support than I mustered from previous literature. However, here I will focus on some areas of disagreement.

One subtle disagreement relates to the brain representation of the focus of attention. Ruchkin et al. (sect. 5, last para.) state,

We assume that the "number of pointers" is limited (i.e., the amount of information that can be in the focus of attention is limited). Consequently . . . we attribute properties such as short-term memory capacity and displacement of information mostly to the functioning of the prefrontal system.

Instead, Cowan (1995, Ch. 8) distinguished between the mechanisms of the *control* of attention (heavily involving frontal areas) versus the *focus* of attention (heavily involving inferior parietal areas). This distinction matches evidence of the existence of anterior and posterior attention systems (Posner & Rothbart 1991). It considers that the parietal areas are loci for the convergence of information from all senses, making them suitable as multisensory integration areas, and that damage to these areas typically results in deficits of awareness, such as unilateral neglect and anosognosia.

My question about the pointer metaphor is whether the limit is how many pointers the frontal lobe can contain, or how much integrated information can be represented, to which frontal mechanisms can point. Perhaps one testable distinction is whether frontal damage results in a decrease in the capacity of the focus of attention, or only a decrease in the ability to maintain and shift that focus. Several theoretical suggestions for the mechanisms of capacity limits rely on the concept of confusion resulting from overlap in the representations of multiple chunks kept active concurrently (e.g., Luck & Vogel 1998; Usher et al. 2001), favoring the placement of capacity limitations in the posterior representational system rather than the frontal control system.

Another issue pertains to the classification of theoretical views. According to Ruchkin et al. (sect.1.1, last para.),

Baddeley (1986; 2001a; 2002) posited that the working memory short-term storage modules are separate from long-term memory storage modules.

and (sect. 1.2, first para.).

Investigators such as Crowder (1993) and Cowan (1995; 1999; 2001) have been proponents of a contrasting view of short-term memory operation, namely, that long-term memory and short-term memory are different states of the same representations.

The latter position was termed *proceduralist* because the memory representation uses the same neural systems (procedures) involved in perception. I agree but, interestingly, my view has more often been considered similar to that of Baddeley and different from that of Crowder. Baddeley and I have differed from Crowder on the role of memory decay in short-term memory, a concept that Ruchkin et al. invoke to define how long activation lasts.

Decay can be conceived of as the loss of information from memory as a function of time (as in radioactive decay). There is a question of whether short-term memory representations do decay. I have posited so in most of my theoretical writing, whereas Crowder (1993) has eschewed that concept. According to Crowder (also Nairne 2002), the loss of information over time occurs only because the most recent information loses distinctiveness in memory. The common analogy is that if one stands near a telephone pole and looks down a long series of poles (a metaphor for a stimulus list), the nearest few poles look more distinct from one another than do farther-away poles. However, if one moves to a point far beyond the end pole (a metaphor for a long retention interval in a memory test), even the end pole begins to blend in with the others.

Although my colleagues and I have addressed this issue in several studies, the existence of decay is as yet neither proved nor disproved. In support of decay, Cowan et al. (1997) examined two-tone comparisons and found that performance decreased as a function of the time between tones, even when it was expressed as a ratio between that time and a prior inter-trial interval. However, when we reexamined the data to consider previous intervals in the trial series, we could not totally dismiss the possibility that information is lost at a rate that depends on prior intervals (Cowan et al. 2001). This method warrants more systematic investigation.

Baddeley's (1986) conception of working memory relies upon the assumption of decay of the short-term representation and bases that assumption on the finding that the serial recall of words depends upon the spoken durations of those words. For lists of long words there is more time for decay during rehearsal (or during recall; Cowan et al. 1992). Recent evidence suggests that, when one matches linguistic properties of lists of words that can be spoken quickly versus less quickly, word-length effects are unreliable (Lovatt et al. 2002; Service 1998). However, those studies involve only modest differences in the spoken durations of short and long words. In contrast, the original word-length effect was based on lists of monosyllabic words versus words with larger numbers of syllables, which produce much larger differences in spoken durations. Although one cannot use these uncontrolled stimuli to establish a time-based effect, Cowan et al. (2000) demonstrated word-length effects in comparisons of the identical word lists under instructions to speak quickly versus much slower.

Without decay, the notion of activation still can be preserved by assuming that it ends through displacement of one representation by another (cf. Atkinson & Shiffrin 1968). Supporting this idea, some amnesiacs retain story information for up to an hour if no other stimuli intervene, even after sleeping during the retention interval and therefore clearly not rehearsing the story continually (Della Sala et al., in press). A type of memory activation thus may preserve the most recent information for long periods.

The unitary view of short-term memory (Nairne 2002) and its precursor, interference theory, hold that short- and long-term

memory phenomena follow common rules. This goes well beyond the version of the proceduralist assumption held by Ruchkin et al. It repudiates not only separate short-term memory structures (Baddeley 1986; 2002), but also separate short-term memory processes. In defense of dual processes, Broadbent (1971) argued that we should, in fact, expect short- and long-term memory results to resemble each other, given that short-term memory is heavily involved in creating long-term memories. Cowan (1995; 2001) described how short- and long-term memory results differ in subtle ways.

Thus, psychological theory is more than dichotomous. The view of Ruchkin et al. resembles unitary memory theory in denying the existence of separate short-term memory structures, but differs in retaining separate short- and long-term memory processes. I agree, though I remain unsure of the nature of activation and capacity limitations. Regardless, the target article compellingly demonstrates the usefulness of electrophysiological techniques for understanding psychological processes.

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Some mechanisms of working memory may not be evident in the human EEG

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Abstract: Ruchkin et al. use brain-activity data from healthy subjects to assess the physiological validity of a cognitive working memory model and to propose modifications. The conclusions drawn from this data are interesting and plausible, but they have limitations. Much of what is known about the neural mechanisms of working memory comes from single neuron recordings in animals, and it is currently not fully understood how these translate to scalp recordings of EEG.

In this commentary, I outline four types of physiological limitations to what can be concluded from the existing brain-activity data, such as that used by Ruchkin et al.

First, our current knowledge about the neural underpinnings of scalp-recorded EEG signals is not enough to conclude that a neural phenomenon does not exist. Is it legitimate to rule out the existence of specialized short-term memory buffers because their signatures are not evident to us in the EEG phenomena we select? This is especially difficult to judge, as we do not yet have a sufficient understanding of the basic neural mechanisms that underlie cognitive concepts such as “representation” and the “activation” thereof, let alone their reflections in the scalp EEG. Ruchkin et al. suggest that activations of semantic representations, for example, might be deduced from modulations of the N400 component. But it is as yet unclear whether the neurophysiological indices of these activations are DC-shifts. Stimulus-specific persistent neural activity as a neural mechanism underlying working memory was discovered thirty years ago, and it is neural firing that is hypothesized to be sustained by synaptic reverberation (Wang 2001). Oscillations of local field potentials associated with such reverberations might give rise to DC-shifts (Caspers et al. 1987), but they might be more directly visualized as EEG oscillations. The extent to which neural firing itself is visible in the scalp-recorded EEG is probably very limited (Logothetis et al. 2001). Ruchkin et al. acknowledge the importance of neural oscillations, but they limit their use to assessing interareal coupling and prefer DC-shifts as an index of intra-areal processing. Why not treat oscillations as an index of intra-areal processing too? It is quite reasonable to assume that certain types of neural oscillations do not

covary with slow neural changes, such as DC-shifts, and can reveal neural processes that otherwise remain undetected (Düzel et al. 2003).

Second, one element of physiological working memory models in animals is the robustness of delay activity to distracters (Miller et al. 1996). For example, the Miller et al. study showed persistent stimulus-specific neural firing in inferotemporal cortex as well as prefrontal cortex (PFC), but only the prefrontal activity was robust to distracters in the delay or retention interval. This finding suggests that PFC neurons can maintain stimulus-selective delay activity even when delay activity in inferotemporal regions is disrupted by intervening distracters, which in turn might suggest that stimulus-selective delay activity in PFC does not require delay activity in temporal or posterior brain regions (Goldman-Rakic 1995; Wang 2001). Currently we cannot tell if the DC-shifts recorded by Ruchkin et al. would also show robustness to distracters.

Third, animal studies suggest that prefrontal neurons code information in working memory that is more than a “pointer” to posterior stimulus-specific delay activity. My understanding of how Ruchkin et al. view “pointers” is that these do not store stimulus-selective information. Rather, they index where stimulus-selective information is stored. However, there is evidence that prefrontal neurons indeed store stimulus-selective information and that, contrary to what Ruchkin et al. assume, the firing patterns of prefrontal and parietal neurons could be compatible with duplication of information in both regions. A direct comparison of prefrontal and parietal delay activity in nonhuman primates in a spatial working memory task has shown that neurons in both cortical areas exhibit very similar sustained activity during the delay period, with nearly identical spatial tuning (Chafee & Goldman-Rakic 1998). This finding means that different prefrontal neurons have different spatial selectivity in the delay period and hence can code stimulus-specific information to an extent that is likely to go beyond being a mere pointer to other representations.

Fourth and finally, brain-activity data in healthy subjects cannot identify brain processes that are critical for a given cognitive function. Are the posterior DC-shifts that Ruchkin et al. have related to the maintenance of stimulus-specific information, epiphenomenal, or do they reflect critical processes for working memory? From Ruchkin et al.’s model this question will be difficult to test, because the model suggests that delayed maintenance of stimulus-specific information is accomplished in those brain regions that initially process the task-relevant aspects of the stimulus. A permanent lesion in such brain regions would impair stimulus processing even before any maintenance operation could start. What is necessary to answer this question, are “dynamic” lesions, which cause impairment selectively and transiently during maintenance. One way to achieve such dynamic lesions in humans would be by transcranial magnetic stimulation (TMS) (Düzel et al. 1996) applied during the retention interval over the areas where the posterior DC-shifts occurred in the Ruchkin et al. study. Two recent TMS studies are relevant in this respect. Both of them show that TMS over posterior neocortex disrupts working memory, but only if it is applied early, close in time to stimulus processing, and not later in the retention interval (Harris et al. 2002; Oliveri et al. 2001). One study shows that frontal TMS disrupts working memory only when applied later in the retention interval (Oliveri et al. 2001). These results are compatible with frontal areas acting as working memory stores and posterior areas acting as initial processors rather than regions of activated representations.

Prefrontal cortex and the generation of oscillatory visual persistence

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Abstract: In this commentary, the formation of “pre-iconic” visual-prime persistence is described in the context of prime-specific, independent-component activation at prefrontal and posterior EEG-recording sites. Although this activity subserves neural systems that are near identical to those described by Ruchkin and colleagues, we consider priming to be a dynamic process, identified with patterns of coherence and temporal structure of very high precision.

Neural oscillations in electrophysiological investigations are found throughout the cortex at a wide range of frequencies and at every level of resolution. The extent to which the brain appears to employ oscillations, the variety and complexity of oscillatory structures challenge any precise description of their functional role. If we are to consider the timing of neural activity as an organic instantiate of (inner) psychophysical processes at work, with a physical structure that allows correspondences to be made between these levels of analysis, then “precise description” may be considered to refer to which specific characteristics of neural timing relate to which characteristic of the psychophysical process under examination. Good temporal frequency resolution in the EEG provides a means of resolving this problem by permitting correspondences to be made between the timing of neural events and

observations of behavior. Considered from the psychophysical perspective, perhaps the optimal conditions to address this question are those in which perception becomes influenced by variations in the temporal characteristics of stimulus events. However, the majority of psychophysical methods employed are conceptually static in nature, whereas the questions addressed here, namely the relation of memory storage with the binding of activity across neural mechanisms, explicitly aim at dynamic aspects of psychophysical structure.

Is there evidence for dynamic psychophysical structure related to temporal binding? One line of evidence relates to the sub-threshold, oscillatory-priming effects reported by Elliott and colleagues (Elliott & Müller 1998; 2000; Kompass & Elliott 2001). Prime responses exhibit certain temporal characteristics: Primes persist for a duration shorter than that of iconic memory, but consistent with the persistence of a visible stimulus (i.e., ≤ 300 msec; see Coltheart 1980); and they are periodic, characterized by the frequency of priming-display presentations (e.g., the prime reaction time [RT] \times premask-target ISI functions were periodic with a frequency of around 40 Hz; see Elliott & Müller 2000). That prime persistence comes to be characterized by the frequency of prime-display presentation (the priming stimulus comprises one of four repeatedly presented but asynchronized image frames, each presented at 10 Hz) has been taken as an indication that the prime is generated by mechanisms capable of coding global stimulus properties in interaction with relatively early visual-coding mechanisms. A second line of evidence, which supports this view, draws from the observation of Kompass and Elliott that the prime response temporally precedes regular, priming-stimulus presentation, and – given presentation at an identical phase relative to the rhythm of priming display presentation – also precedes target-

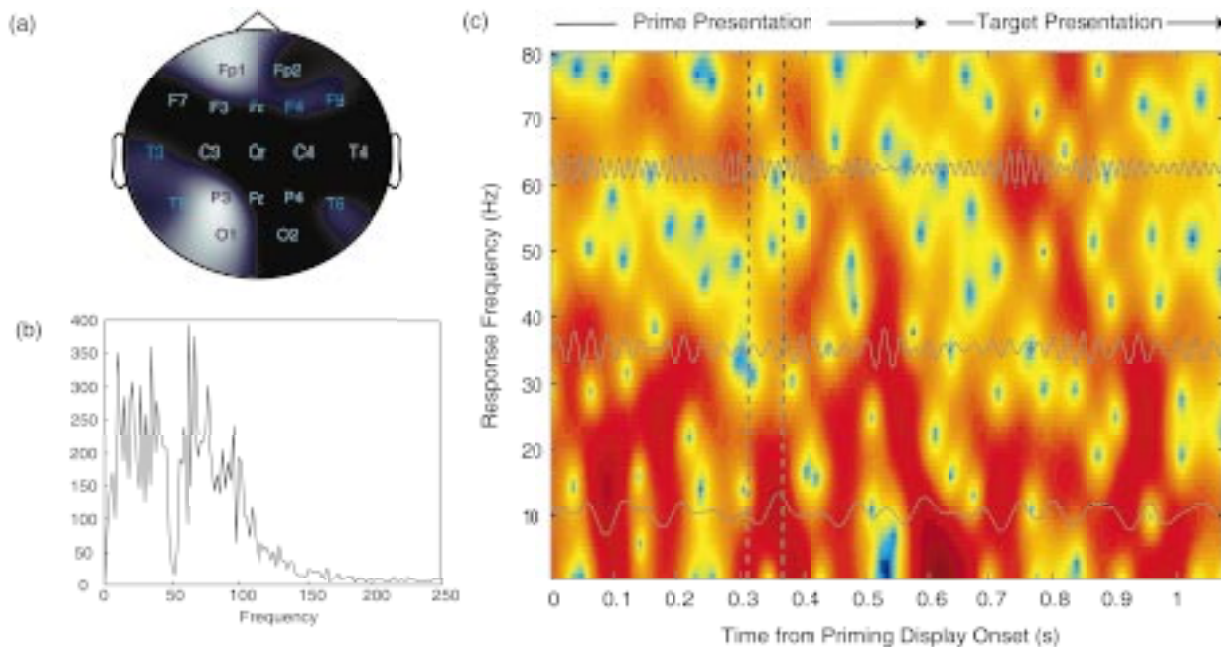


Figure 1 (Elliott et al.). Prime-specific activation during priming-display presentation. In (a) the head plot represents the average distribution of variance across the scalp at the mean time of maximum variance, which occurred at 341 milliseconds (msec) postpriming display onset (light–dark indicates maximum–minimum absolute variance). Averages were calculated from separate components from 10 subjects derived from a series of independent-components reconstructions of the averaged event-related potentials (ERPs) for each of 12 subjects. Clustering automatically excluded two subjects who showed no variance maxima with an appropriate latency or topography. Prominent are maxima under posterior electrodes O1 and P3 and electrode Fp1, which lies approximately over the superior frontal gyrus (Homan et al. 1987) and is associated with dorsolateral prefrontal activation. In (b) is shown the averaged spectral power representation of the 10 component activations. Peaks are evident at 10, 35, and 62/66 Hz. In (c) the spectrogram represents the time-frequency decomposition of the average component activation (blue–red indicates minimum–maximum log variance). The vertical dashed lines illustrate the time range over which variance maxima were clustered (the mean time [and standard deviation] was 341 [29] msec). Horizontal traces represent (in ascending order) the averaged representation of oscillatory activity at 10, 35, and 62 Hz. Times of priming-display and target-display presentation are indicated at the top of panel (c).

display presentation by some tens of milliseconds. In this case, the prime is understood to involve an anticipatory response in higher cortical mechanisms, which serves to “preactivate” lower level prime- and target-coding mechanisms.

Evidence for multiregional prime activity with particular temporal characteristics may also be drawn from examination of the EEG¹ accompanying priming-stimulus presentation. Component activations reconstructed from the EEG provide evidence for prime development as the combined function of occipito-parietal and prefrontal cortical activation. This is shown in Figure 1. Here component activity consists of coactive neural assemblies located under electrodes Fp1 and O1/P3. One function of prefrontal cortex is a delayed sample to matching response and it seems likely that the coactivation necessary for coding repeated prime presentation, in terms of the global frequency of priming-stimulus presentation, might be carried out by assemblies under Fp1 responding to a staccato of 10-Hz signals from posterior assemblies coding the local spatio-temporal organization of the priming display. Of particular interest is the timing of the oscillatory response to priming-display presentation. Notice in Figure 1(c), at the intersection of horizontal traces of high frequency (35 and 62 Hz) activity within the time period of maximum variation lie on, or just after a brief loss of coherence and prior to a subsequent burst of coherent oscillatory activity. From ontogenesis > 66 Hz at 400 msec, coherence spreads across lower frequencies as a function of time. Related activity occurs in the 35–40-Hz region at around 530–540 msec with corresponding activity at around 10 Hz at 590 msec, almost immediately prior to target-display presentation at 600 msec. The pattern of coactivation between neural assemblies under Fp1 and O2/P3 thus offers itself as a strong candidate for generation of the anticipatory response reported by Kompass and Elliott (2001).

Two points emerge from the analyses presented here. The first is that prefrontal-posterior synchronization appears to be involved in the formation of stimulus-related persistence, which has been shown to possess a duration sufficiently short to suggest that coactive neural assemblies may remain functional for as little as 200–300 msec post-stimulus offset (Elliott & Müller 2000). The second is that at least one characteristic of the prime response, the temporal precession of prime activity relative to target display presentation, may emerge as a function of cascading fluctuations in coherence between various frequency responses to prime stimulus presentation. An identification of particular dynamic states, which appear to be related to particular psychophysical performance, refocuses attention towards the requirement for description of active cognitive states in terms of the dynamic states upon which they may depend.

NOTE

1. For 12 subjects (4 male, mean age 24.1 years) the EEG was recorded from 19 Ag-AgCl electrodes (electrode positions are shown in Figure 1(a)) according to the international 10–20 system. Subjects performed a variant of the primed target detection task described in Elliott and Müller (1998). The experiment described here employed a priming-display presentation frequency of 40 Hz while priming displays were presented for 600 msec and followed immediately by target-display presentation. The electrodes were mounted in an elastic cap, were referenced to Fz while the nose served as the ground electrode. Electrode impedance was maintained below 5 kOhm. Horizontal and vertical electrooculograms (EOG) were additionally registered with four electrodes. EEG activity was amplified by means of NeuroScan amplifiers, digitized on-line with a sampling rate of 500 Hz and analog-filtered with a 0.1-Hz high-pass and a 100-Hz low-pass filter. A 50-Hz notch filter was applied to remove artifacts related to the main's electricity supply.

For the recording of EOG, the time constant 300 msec with a low pass filter at 70 Hz was used. The EOG-channel was visually inspected for each trial, and trials with eye movement or blink artifact were rejected. Localized muscle artefacts (at electrodes T3 and T4) were identified and if present reconstructed by means of an extended independent components analysis (ICA) algorithm (see Makeig et al. 1999). Averaging epochs lasted from termination of an alerting tone 200 msec before until 1,200 msec after priming-display presentation. Baselines were computed in the – 200

to 0 msec interval for each trial and subtracted prior to subsequent analyses. Analyses were carried out on the averaged event-related potential (ERP) for each subject.

In a first step, a series of component activations were recovered from each averaged signal by means of ICA using information maximization (infomax) techniques described by Bell and Sejnowski (1995) with variants of the ICA Matlab package (v.3.52) (available at: <http://www.cnl.salk.edu/~scott/>). In order to classify components and identify particular groups of clusters that appeared during premask-matrix presentation, components were defined in terms of the latency and topographical distribution of variance maxima (in this case, topographical projections were standardized by substituting raw activation at each electrode with the corresponding *z*-value computed relative to all projected activations at the time of maximal activation). Classification then proceeded by means of cluster analysis, calculating Euclidean distance between objects and computing linkages in a hierarchical cluster tree based upon the average distances between groups of objects and a threshold of 19 clusters (cophonetic correlation coefficient *c* = 0.81). The resulting clusters were considered for further analysis if (i) they included activations from more than 75% of subjects (i.e., 9 or more of 12 activations), (ii) they were specific to priming-stimulus presentation, (iii) maxima fell within the period of priming-display presentation, and (iv) if, following examination of the frequency component of each component activation by means of a 256-point fast-Fourier transform (FFT), strong peaks were evident at, or close to the priming-display presentation frequency of 40 Hz. On these criteria, a single component cluster was identified, which is described in Figure 1 and the main body of text.

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Thoughts from the long-term memory chair

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Abstract: With reference to Ruchkins et al.'s framework, this commentary briefly considers the history of working memory, and whether, heuristically, this is a useful concept. A neuropsychologically motivated critique is offered, specifically with regard to the recent trend for working-memory researchers to conceptualise this capacity more as a process than as a set of distinct task-specific stores.

In this interesting article, Ruchkin and colleagues tackle the important question of whether working memory reflects the activation of long-term memory. They advance a parsimonious “activation-proceduralist” framework, in which they specify that long-term memory systems associated with posterior cortical regions provide the necessary representational basis for working memory, and that the prefrontal cortex provides the necessary attentional control. In so doing, the authors argue that there is no reason to propose the existence of specialized neural systems whose functions are limited to short-term memory buffers, and they raise related and important issues concerning whether working memory is itself a useful concept. This is an ancient and significant debate. William James (1890) drew the distinction between primary and secondary memory, regarding the former as the “rearward portion of the present space of time” as distinct from the “genuine past.” Later, in the second half of the twentieth century, it was suggested that the short-term store might use phonological coding (as indicated, e.g., by Conrad's phonological confusability effect), whereas long-term memory may be mediated primarily via semantic coding.

In their article, Ruchkin et al. themselves evoke findings and concepts, which, as the authors acknowledge, hark back to some ideas that were articulated several years ago; for example, those proposed by Crowder (1993). Indeed, the influence of what could be termed the “international working-memory lobby” notwith-

standing, one may wonder to what extent Ruchkin and colleagues are targeting something of a straw man here. For example, in recent years there has been a trend for working-memory researchers themselves to conceptualise this capacity more as a process than a set of distinct task-specific stores. These researchers have raised important questions regarding the role of rehearsal in transferring mnemonic information from short-term memory (STM) to long-term memory (LTM), and to observed temporally-mediated differences in the recency effect of serial recall. Furthermore, the distinction between phonological (STM) and semantic (LTM) processing has been challenged by consideration of the processes underlying capacities such as sentence comprehension.

From a different perspective, Ruchkin et al.'s neurologically informed analysis is timely; that is to say, it agrees with some contemporary evaluations of the functional properties of working memory offered by cognitive researchers such as Gordon Brown (cf. Brown 2002; Brown et al. 2000; Neath et al. 1999), as well as by neuropsychological researchers, including Morris Moscovitch and Gordon Winocur (the latter articulating concepts such as "working with memory" in the 1990s; cf. Moscovitch & Winocur 2001). It has been suggested by some recent cognitive researchers, for example, that the demonstration of a working-memory recency effect occurring across different time spans relates to the use of working-memory "scanning," which depends (at least in part) on the exact relationship between items of target information and the background from which they must be discriminated.

Ruchkin et al. raise an important point regarding the claim by Baddeley (2001a) that construing short-term memory as activated long-term memory is inconsistent with neuropsychological data. Furthermore, patients may also show dissociations within the domain of STM; that is, there are demonstrated selective cases of impaired verbal versus visuospatial STM (Basso et al. 1982; Hanley et al. 1991).

There is also some evidence that visual (as distinct from visuospatial) STM can also be selectively impaired (e.g., Davidoff & Ostergaard 1984; Warrington & Rabin 1971), and that phonological and lexical STM deficits may be separable (Martin et al. 1994).

Long-term memory is sometimes preserved in these individuals with STM deficits (e.g., in Warrington & Shallice's (1969) patient, KF, with selective auditory verbal STM loss). Indeed, this is the kind of evidence that has been adduced by researchers such as Baddeley (2001a). However, consistent with the views articulated by Ruchkin et al., the widely held view regarding selective STM loss in some neuropsychological patients has been called into question in situations in which the STM and LTM tests tap into the same type of information (e.g., Baddeley et al. 1988; Hanley et al. 1991), with suggestions that there is, in fact, evidence of serial processing from STM to LTM. Mayes (2000) argues that LTM probably is only selectively preserved when it taps different information from that affected by a STM disorder.

The views articulated by Ruchkin et al. offer significant heuristic value. Indeed, as indicated in the previous paragraph, what may now be emerging in the memory literature is the breakdown of the old primary-STM-WM/secondary-LTM distinction, with an emphasis instead on *function* and *process* (see, e.g., Toth & Hunt 1999; "Not one versus many, but zero versus any"). On a related theme, Roediger et al. (1999) have articulated a component-processing framework of memory, whereas Gordon Brown (personal communication) has provided considerable food for thought in recent years by modelling the diversity of memory phenomena in terms of potentially common processes across previous structural divisions. In conjunction with Gordon Brown, my colleagues and I working in Western Australia have demonstrated that working-memory capacity may also be affected in a selective hippocampal patient with profound long-term memory deficits. More specifically, this patient's poor performance on the primacy portion of serial recall appears to be a result of the fact that (in contrast to controls) he does not rehearse items in working memory when he is encouraged to do so. This may be an informative observation with respect to the framework articulated by Ruchkin et al.

There are some elements of the framework proposed by Ruchkin et al. in which further information would have been useful in order to evaluate the model's explanatory value. For example, when stating that "long-term memory systems in posterior cortex are initially activated for the processing of incoming information" (target article, sect. 5, para. 1), it would be useful to know explicitly whether these LTM systems are deemed to be semantic systems, episodic systems, or both. Or, indeed, whether a systems framework is embraced at all by the authors, and, if so, which one? (See Foster & Jelicic 1999, for a discussion of this complex question.) On the related theme of memory systems, to what extent are implicit, as distinct from explicit, memory representations drawn upon in mediating working-memory processes, according to this framework? Ruchkin and colleagues further state that "as stimuli are perceived and processed in posterior cortex, long-term memory codes are activated" (sect. 5, para. 2). Yet, there is considerable ongoing debate in the literature regarding the representational nature of these LTM codes.

More specifically, there is currently substantial debate regarding the significance of context in the neural representation of established memories. It would have been useful to know whether this is a relevant consideration for the kinds of posterior memory systems that are specified by Ruchkin and colleagues. On a related note, to what extent is the medial temporal lobe memory system deemed relevant in this model? The authors state,

the neural systems that ultimately become the repositories of the consolidated long-term episodic memory for the novel information are initially active, with the hippocampus providing coordinate control. In this view, short-term episodic memory consists of well-consolidated and partially consolidated long-term episodic memories in an active state.

Yet, according to the conventional consolidation hypothesis, memories are "downloaded" from the hippocampus to the neocortex over time. If the hippocampus is considered relevant for the Ruchkin et al. framework, as appears to be the case, to what extent would it be possible to identify the involvement of this circumscribed brain region using an ERP methodology, given some of the localization issues that the authors themselves identify in the Appendix? To what extent, in this framework, is attention considered to be related to or distinct from memory rehearsal processes, specifically regarding the proposed role of the prefrontal cortex in subserving "attentional control." Are prefrontally-mediated mechanisms the only factors of consideration when evaluating the basis of short-term memory *capacity*, or may posterior cortical constraints be relevant as well (i.e., aside from those matters relating to working-memory decay specified by Ruchkin et al.). The authors state, "Recall and maintenance of episodic information involves activation of the binding circuitry; retention of novel episodic information involves the operation of binding formation and the initial consolidation process" (sect. 1.3). However, the significance of these statements is unclear as written, and further elaboration is required.

Missing the syntactic piece

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Abstract: The notion that the working-memory system is not to be located in the prefrontal cortex, but rather constituted by the interplay between temporal and frontal areas, is of some attraction. However, at least for the domain of sentence comprehension, this perspective is promoted on the basis of sparse data. For this domain, the authors not only missed out on the chance to systematically integrate event-related brain potential (ERP) and neuroimaging data when interpreting their own findings on semantic aspects of working memory, but also neglected syntactic aspects of working memory and computation altogether.

Ruchkin et al. argue that the so-called working-memory system is not a separate system located in the prefrontal cortex, but that the prefrontal cortex only provides the attentional pointer system for maintaining activation in posterior long-term memory systems. Although the idea that particular memory representations are not moved from posterior to frontal areas during active maintenance is compelling, the data presented in its support is unnecessarily sparse – at least for the domain of sentence processing.

The present commentary argues that a less speculative claim with respect to the functional specificity of posterior and frontal areas during sentence processing and retention could have been made if imaging data had been incorporated more systematically. When discussing the issue of sentence processing and working memory, Ruchkin and colleagues first choose to focus only on semantic aspects of sentence processing, rather than also taking into account syntactic parameters, and second, refrain from relating their own data on semantic parameters to available imaging studies.

Although the authors admit that sentence comprehension involves processes of semantic and syntactic binding, they consider the number of “propositions and the thematic role relations they express” (sect. 3.7, para. 2) and the semantic short-term memory processes thus drawn upon, to be of crucial relevance during language comprehension. This may well be the case when considering the *postsentence retention interval*, but not necessarily when considering *on-line sentence processing*. Rather, it appears that syntactic aspects of working memory are of major relevance during sentence comprehension, in particular when the sentence is syntactically complex. Thus, it has been shown that additional working-memory resources are necessary when comprehending syntactically complex compared to syntactically simple sentences, even when the number of propositions remains the same (Cooke et al. 2001; Fiebach et al. 2001; 2002). Syntactic working memory, in this context, can be operationalized as a function of the distance between two critical positions in a given sentence. In object-first sentences, for example, the object noun phrase (the “filler”) is moved away from its original position in the sentence, leaving behind a trace (the “gap”). During on-line sentence processing the system first encounters the object noun phrase (filler), which, however, must be maintained in working memory until the original object position (gap) is encountered. A long filler-gap distance thus requires more syntactic working-memory resources than a short filler-gap distance. In an event-related brain potential study, Fiebach et al. (2002) demonstrated that a left frontal sustained negativity was observable between the filler and its gap, but not beyond the gap position. This finding suggests that it is syntactic working memory (i.e., maintaining the filler in working memory until its original position in the sentence is encountered) that involves left prefrontal areas. Note also that, in this study, the semantic content of fillers was minimal, thereby excluding the possibility that the sustained negativity reflects semantic aspects of maintenance. In a functional magnetic resonance imaging (fMRI) study (Fiebach et al. 2001) using similar materials, it was found that activation of the left inferior frontal gyrus, more specifically BA44 and BA44/45, varied as a function of syntactic working memory (distance between filler and gap). Interestingly, activation in the superior and middle temporal region also increased as a function of this factor. A further fMRI study used sentences of increasing syntactic complexity as induced by dislocated noun phrases that had moved only a small distance (Fiebach et al., in press). A parametric analysis indicated that the activation of BA44 selectively increased as a function of syntactic complexity, thereby suggesting that, although syntactic working memory may involve inferior frontal and temporal areas, BA44, in particular, holds responsible for aspects of syntactic complexity. The temporo-frontal network, including the superior and middle temporal gyri and BA44/45, in contrast, appears to support syntactic working memory. Within this network, the temporal areas most likely provide the knowledge-based identification of lexical and syntactic information, whereas frontal areas subserve the procedures operating over this knowledge (for a review, see Friederici 2002).

A similar view of a temporo-frontal network is proposed by Ruchkin et al. as the basis for short-term memory processes, when they claim that the “short-term memory process evidently depends in part on interactions between frontal and posterior cortex implemented by the operation of frontal-posterior projection loops” (sect. 3.7, para. 3). However, neither empirical evidence nor references are given to support their neuroanatomical statements concerning the projections between frontal and posterior regions. The main data set they base their claims upon is a study by Haarmann et al. (submitted) which is still under review and, therefore, unfortunately inaccessible in any greater detail at present. In this study, sentences containing related nouns were more easily processed than those containing unrelated nouns. For sentences containing related nouns, a sustained negativity over centro-posterior sites is reported, both during sentence processing and during retention. Unfortunately, however, the figure in which the activations for different brain regions are plotted (Fig. 10) only contains the activation for the sentences with the unrelated nouns, and therefore does not allow for a direct comparison of the effect of semantic relatedness on particular brain regions during sentence processing versus retention. As a key finding, the authors highlight their observation that a number of posterior areas were active both during sentence processing and retention. Figure 10, however, suggests that the right posterior middle temporal gyrus increases its activation systematically during the retention phase only. This seemingly contradictory finding is interpreted as being a result of hemispheric differences, with more fine-grained semantic processes in the left hemisphere being active during sentence processing and coarse semantic processes in the right hemisphere being active during retention. An alternative interpretation of the differential hemisphere involvement, which is moreover supported by a number of fMRI studies on sentence processing, is that on-line sentence processing requires more syntactic resources localized in the left hemisphere than retention of meaning (Dapretto & Bookheimer 1999; Friederici et al. 2003; Kuperberg et al. 2000; Newman et al. 2001, Ni et al. 2000). More generally, the observation that sentence comprehension involves a much greater degree of syntactic processing than retention, appears problematic for the authors’ assumption that similar representations are activated during sentence comprehension and retention. Finally, the authors only loosely interpret activation in additional brain areas, without taking into consideration available fMRI findings. The right prefrontal cortex and left insular activation is not even functionally discussed, although the former area has been shown to reflect aspects of episodic memory (e.g., Düzel et al. 1999; Wiggs et al. 1999), and the latter has been shown to increase as a function of retrieval effort (e.g., Buckner et al. 1996; 1998), two aspects worth considering in the present context.

In conclusion, we have identified two insufficiencies in the application of Ruchkin et al.’s approach to language comprehension. On the one hand, the authors only loosely relate their own findings to recent fMRI studies and, on the other hand, they disregard syntactic aspects of working memory and sentence comprehension altogether. This weakens their description of sentence processing and retention, though not their general view that the posterior and prefrontal cortex work together during working memory.

More than working memory rides on long-term memory

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Abstract: Single-unit data from the cortex of monkeys performing working-memory tasks support the main point of the target article. Those data, however, also indicate that the activation of long-term memory is essential to the processing of *all* cognitive functions. The activation of cortical long-term memory networks is a key neural mechanism in attention (working memory is a form thereof), perception, memory acquisition and retrieval, intelligence, and language.

For reasons that Ruchkin et al. allude to in the target article, their thesis – that short-term memory is activated long-term memory – resonates well with our single-unit data. Here I will briefly dwell on those data with a dual purpose: to strengthen that thesis and to expand the memory-activation idea beyond the focus of the article. I think the latter is necessary to put both short- and long-term memory in the proper neurobiological perspective. Indeed, the activation of long-term memory is a plausible neural mechanism of working memory, but then, this can also be said of *any* other cognitive function, however simple or complex, however mundane or arcane.

We have investigated the activity of cells in the prefrontal, parietal, and temporal cortex of the monkey during performance of numerous working-memory tasks. In such tasks, we have had our animals remember visual, spatial, tactile, or auditory memoranda. An important consideration is that, for a period of months prior to unit recording, the animals have been extensively trained to perform their task(s). Therefore, at the time of cell recording, the tasks, the guiding cues, and the reward for good performance can be assumed to be securely consolidated in the long-term memory of the animal. The most general conclusions from our unit studies (Fuster 1995) are the following. (1) Any cue or memorandum to be remembered in working memory, of whatever sensory modality, elicits cell reactions not only in cortical areas devoted to the processing of stimuli of the cue's modality, but also in areas dedicated to other modalities. (2) Many cells are activated not only in the working-memory period of performance ("delay"), but also, or instead, in the periods of perception or recognition of the cues, when the animal must encode a stimulus for short-term retention, or else, recognize it for appropriate choice and behavioral response. (3) Cell reactions to a given stimulus correlate with reactions to another stimulus that has been behaviorally associated with it by learning, even if the two stimuli are of different modality (e.g., auditory and visual, visual and tactile). (4) Correct behavioral performance correlates with level of cell discharge during perception and/or retention of a cue; distracting stimuli interfere with both performance and cellular activation.

Although our unit studies are considerably less than exhaustive in terms of cues, tasks, cell numbers, and cortical areas, the four conclusions listed above appear to be generally valid; and so we can posit the following, more general conclusions, which are otherwise supported by a large body of neuropsychological and neurophysiological evidence (Fuster 2003). The long-term memory of a task and the stimuli that guide it are encoded in a vast network of cortical cell assemblies that represent all the associated features of the task and its guiding stimuli. Those cell assemblies are anatomically dispersed in primary sensory and motor cortex, as well as in cortex of association. The same is true for declarative memories, whether episodic or semantic. Every memory is made of a network of cortical neurons representing the associated components of that memory. The cortical memory code, therefore, is a relational code. An item of knowledge or memory in long-term storage (which I call a *cognit*) is essentially defined by the connections between the neurons of a distributed cortical network. Memory networks overlap and intersect at many points or neu-

ronal nodes. Consequently, a cell or group of cells, practically anywhere in the cortex, can be part of many networks, and thus of many memories.

All cognitive functions, including the formation and retrieval of memory, consist of the activation of one or several memory networks and the temporal transactions within and between those networks. Those transactions, which consist essentially of a coordinated succession of excitatory and inhibitory synaptic exchanges between cortical neurons, constitute the *dynamic* basis of attention, perception, intelligence, and language. The *structural* basis for all those functions is long-term memory, a vast array of cortical networks formed by prior experience and the consequent synaptic modulation. In psychological terms, what we call working memory or active short-term memory is an operational definition of attention, that is, of the selective allocation of neuronal assemblies and networks of long-term memory to the processing of current behavior. Essentially, working memory is attention focused on an internal representation, that is, on a representation stored in long-term memory that, at a given time, has been activated and updated for the performance of a particular task or sequence of acts.

Perception is also based on long-term memory. Every percept of the world around us is an "interpretation" of current sensory data in the light of our experience with similar data stored in long-term memory. Thus, perception has been appropriately called the testing of hypotheses about the world. We not only remember what we perceive, but also perceive what we remember. Perceiving must essentially involve the matching of external gestalts to internalized representations in long-term memory. There cannot be an entirely new percept, because any conceivable new sensory configuration can resonate by associations of similarity or contiguity with others in long-term storage, which the new experience modifies and updates. In other words, the new experience modifies and updates previously established cortical networks. Intelligence and language, in all of their manifestations, operate in basically the same way, that is, by the activation of long-term memory networks towards the processing of intelligent behavior or speech.

In sum, this commentary is intended not only to support the inference on working memory that Ruchkin et al. draw from their data, but also to extend the validity of that inference to other cognitive functions. Perception, the acquisition and retrieval of memory, language and intelligence, as well attention – including working memory – depend on the selective and orderly activation of long-term memory networks in the cerebral cortex.

From working memory to long-term memory and back: Linked but distinct

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Abstract: Neural models have proposed how short-term memory (STM) storage in working memory and long-term memory (LTM) storage and recall are linked and interact, but are realized by different mechanisms that obey different laws. The authors' data can be understood in the light of these models, which suggest that the authors may have gone too far in obscuring the differences between these processes.

Ruchkin et al. argue against the idea that STM and LTM are realized by different systems, and that "long-term memory and short-term memory are different states of the same representations, with activated representations in long-term memory constituting all of short-term memory" (target article, sect. 1.2). This claim is restated in various ways; for example, "short-term memory maintenance of the items consists of reactivation of the long-term memory representations" (sect. 3.8). I suggest that these claims are not entirely true, even though they overcome an even greater

error. Three decades of neural modeling of behavioral and brain data about STM and LTM (e.g., Bradski et al. 1994; Brown et al. 1999; Carpenter & Grossberg 1991; Fiala et al. 1996; Grossberg 1968; 1980; 1982; 1987; 1988; 1999; Grossberg & Myers 2000; Grossberg & Williamson 2001; Page 2000) suggest that STM and LTM are intimately linked, but embody different organizational principles, are realized by different mechanisms, and obey different laws. Available models clarify cellular neural mechanisms of STM/LTM and their integration into brain systems – including how STM per se differs from prefrontal working memory – that can temporarily store multiple events and their order in STM.

STM involves activation of cells that receive signals from axons whose synapses contain adaptive weights which encode LTM. Suitable (but not all) cell activations in STM can lead to learning and LTM within abutting synapses whose axons are active at that time (associative learning). Later activation of these axons can read out LTM into cellular STM activations. Although this description clarifies why STM and LTM are closely linked, it does not completely support the authors' claim that "long-term memory and short-term memory are different states of the same representations." To see this, imagine that two different sets of cells read-out their LTM into the same target cells at different times. Then the STM patterns that develop will be different. STM combines LTM read-out from multiple cells into a composite STM pattern. Moreover, "short-term memory maintenance of the items" does not necessarily consist "of reactivation of the long-term memory representations." STM can be maintained by recurrent interactions that are different from those which read-out LTM. Indeed, a key role for working memory is to temporarily store an unfamiliar sequence of events before learning can chunk it into a new LTM representation.

Working memories cannot work well unless they operate at correctly defined processing levels and obey correctly constrained laws. Many experiments support the proposal that a working memory represents sequences of "items" that have individually been unitized through prior learning experiences. Familiar feature clusters that are presented within a brief time interval become items by being categorized, or unitized, in LTM at a processing stage that occurs before the working-memory stage. As item categories are processed through time, they input to a working memory in which multiple items are simultaneously stored as part of an evolving spatial pattern of activation across a network of item representations. This spatial pattern represents both item information (which items are stored) and temporal order information (the order in which they are stored). Individual items can be recalled when a rehearsal wave nonspecifically activates the entire working memory. The rehearsal wave allows the most active items to be recalled first, after which they inhibit their own representations using recurrent inhibitory feedback, so that less active items can also be recalled in the order of their relative activity (Grossberg 1978a; 1978b; 1982; Koch & Ullman 1985; Page & Norris 1998).

A number of articles have modeled such "item-and-order working memories" to explain data about free recall (Bradski et al. 1994; Grossberg 1978a; 1978b; Page & Norris 1998), reaction time during sequential motor performance (Boardman & Bullock 1991; Grossberg & Kuperstein 1986/1989), errors in serial item and order recall that are a result of rapid attention shifts (Grossberg & Stone 1986a), errors and reaction times during lexical priming and episodic memory experiments (Grossberg & Stone 1986b; McLennan et al. 2003), data concerning word superiority, phonemic restoration, and backward effects on speech perception and word recognition (Cohen & Grossberg 1986; Grossberg & Myers 2000), and so forth. All of these working memory models satisfy two simple postulates (Bradski et al. 1994; Grossberg 1978a; 1978b).

The key postulate, called the "LTM Invariance Principle" proposes how working memories, which encode a type of STM, enable unitized representations of lists of items to be stably learned and stored in LTM. Thus STM and LTM are linked, but in a way

not described by the authors, and one that does not conflate their different roles. For example, after learning the words MY and SELF, suppose that the word MYSELF is temporarily stored in working memory for the first time. How does a listener learn a new word representation for MYSELF without erasing the previously learned word representations for MY and SELF from LTM? When such learning occurs in an unsupervised fashion in real time, as it does when a child learns a language, a poorly designed working memory could easily cause catastrophic forgetting of MY and SELF when learning MYSELF.

The second postulate requires that the maximal total activity of the working memory is finite and, indeed, independent of the total number of active cells. This postulate implies the limited capacity ("the number of pointers"; see target article, Abstract) of working memory. Because total working-memory activity cannot increase indefinitely with the number of activated cells, some cells must be inhibited to enable other cell activities to be stored.

Such working memories are called STORE (Sustained Temporal Order REcurrent) models. Remarkably, specialized recurrent on-center off-surround networks satisfy both STORE postulates. Recurrent on-center off-surround networks are ubiquitous in the brain because they enable distributed input patterns to be processed without a loss of sensitivity by their target cells (Grossberg 1980). Thus, designing a working memory reduces to specializing an ancient neural design. This design is not, however, the same as the design of LTM at the synapses that connect cells at which STM occurs. Properties of synchrony, attention, and consciousness naturally emerge in neural systems that respect these differences between STM and LTM (Grossberg 1999).

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More memory?

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Abstract: Modern investigators of cognition ask about the conditions under which faculties occur rather than about their existence. This tendency, combined with the axiom of parsimony, emphasizes a paradigm shift in the fundamental principles of economic thought in science, mimicking evolutionary conceptualizations. The Ruchkin model of memory-related brain activity replaces less economic models. From interdisciplinary approaches, proceduralist models for other memory-related processes analogously support this model.

A paradigm shift in scientific investigation has occurred over the last third of the twentieth century. Investigators of cognitive processes are increasingly likely to research the conditions under which faculties can be observed, rather than ask whether and where a cognitive faculty exists (cf. Brown & Campione 1973; Cole & Medin 1973; Grote 2003; and Grote, submitted, on mediation and self-instruction as memory). Principles and procedures shift accordingly. Combined with a much older principle in science, this shift is of relevance to Ruchkin and colleagues' target article. Pearson reminded us, in 1892, that William of Occam's Razor, or the axiom of parsimony, forbids postulating needless multiple existences for describing events (Pearson 1943). It is one of the most fundamental principles of economic thought in science.

Ruchkin and colleagues' proceduralist or activation model economically replaces patterns of activities used by same memory systems for models that postulate the existence of more systems. Ruchkin and colleagues propose that different patterns of brain activity in short-term and long-term memory can describe memory processes without needing storage of memory in additional

subsystems or buffers of short- and long-term memory systems. This description of brain activity results from observing patterns of brain activity under various conditions. In their view, a variety of patterns, activated by fewer systems, accounts for short-term memory as well as for long-term memory processes.

This economy in scientific description may mimic the economy that evolution may have selected for natural events. Allowing many permutations by a few entities, perhaps based on algorithms yet to be described for brain activity, is most elegantly seen in DNA coding. The principle of parsimony functions at the language level of science, as it does at the level of observable events in nature, selected by evolutionary processes. Phylogeny provides for the susceptibility of various patterns to occur in ontogeny under various conditions. In other words, an algorithm pervading functions selected by evolution, may go like this: Multiple patterns in few structures, to account for occurrence under multiple conditions, are more economical than multiple structures to account for a variety of patterns. However, to verify this will take more research on the conditions under which many memory functions occur, including more research on more memory proceduralist accounts of the kind provided by Ruchkin and colleagues.

Within their discipline, Ruchkin et al.'s replications across data figures, across many conditions, and across research results by other investigators, seem to lend convincing support to an economic model of brain activity in memory processes. On an interdisciplinary level, proceduralist or activation models in other memory-related processes analogously support Ruchkin et al.'s model. Grote (submitted) discusses an experimental model of self-instruction as a form of memory mediation, in which procedures can control and account for problem-solving facilitated by prompted self-instruction, sometimes needing procedures for prompting commitment to spend attention to and to remember self-instruction. That model requires no special status for a "self," and it requires no separate cognitive-behavioral or neuropsychological structure or meta-structure to be invoked for more memory, in order to have more economic functioning, in problem-solving. The present commentary welcomes Ruchkin and colleagues' findings as a contribution to clarifying a number of concepts related to memory, including self-control, self-regulation, and especially self-instruction, and for purging the need for extra systems from cognitive-behavioral conceptualizations.

A few additional bits of information, however, would have been useful in Ruchkin et al.'s report – especially some relevant for cognitive-behavioral developmental models. Such models regard the modality-specificity of verbal and visuo-spatial dimensions under different conditions of development to be of importance (e.g., Jones 1973 on the visual, Zeaman & House 1979 on two- and three-dimensional stimuli). Hence, I would have liked to see some information on the age and educational level of participants. I also wondered whether they were different or same cohorts of participants that were represented in the various data figures.

A few more (benign) points of criticism: I missed seeing a figure on semantic *relatedness* (sect. 3.7) for comparison with Figure 10 for semantic *unrelatedness* (sect. 3.7). More information about the unpublished research (cited at the end of sect. 3.2 and in sect. 3.4) – and with which colleagues – could have been given in a note; along with further clarification of the Ruchkin (1997a; 1997b) studies, including mention of the colleagues involved here.

Finally, it would be instructive if "Phreneurology" measurement, such as described in the Appendix, could be schematized in a figure, as it is relevant to and referenced in nearly each figure of the target article. (I deliberately call the measurement "phreneurology," tongue in cheek, because it is peculiarly reminiscent of old phrenological concepts for mapping scalp topographies.)

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Another artificial division – and the data don't support it

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Abstract: Evidence for the contribution of the neocortex to memory is overwhelming. However, the theory proposed by Ruchkin et al. does not only ignore subcortical contributions, but also introduces an unnecessary and empirically unsupported division between the posterior cortex, assumed to represent information, and the prefrontal cortex, assumed to control activation. We argue instead that the representational power of the neocortex is not restricted to its posterior part.

Arbitrary divisions are quite popular in science, and, because they help to structure the respective fields, they might make sense for a certain period of time, even if they ultimately turn out to be wrong. So, for example, quite a substantial amount of research was driven by the idea that short-term and long-term memory are realized by distinct storage systems (Atkinson & Shiffrin 1968). In accordance with a number of previous theories based in the fields of Experimental Psychology (e.g., Anderson & Bower 1973), in Cognitive Neuroscience (Fuster 1997), and in Neural Network Modeling (e.g., McClelland et al. 1995), respectively, Ruchkin et al. want to repudiate the existence of this division. Instead, short-term memory is understood as the activated part of long-term memory.

So far so good, but we nonetheless see a problem in the target article. We do not want to discuss whether one more theory stating the nondistinction between short-term and long-term memory was needed. In the same way, we do not want to dispute the experimental quality of the studies presented – even though in almost all cases the comparisons are confounded by differences in the overall difficulty of the conditions examined. (Therefore, the data do not allow for unequivocal interpretations.) Instead, we want to focus on the theoretical contributions of Ruchkin et al.

The main problem we see is that the authors introduce a new artificial division, namely, between the posterior cortex (the region where the memory representations are assumed to be located) and the prefrontal cortex (where an "attentional pointer system" is assumed to control and maintain the activation in the posterior cortex). For the sake of clarity, we break this idea down into three parts in order to illustrate its implications. In addition, we comment on the basic assumptions behind the artificial division.

According to Ruchkin et al., the cortical memory capabilities are assumed to be restricted to the posterior cortex. There is, however, quite substantial empirical work supporting the idea that the anatomical basis for memory is *not* restricted to the posterior cortex. To give just a few examples, it is assumed that motor representations are stored in the motor cortex and probably in the supplementary motor area (see, e.g., Nyberg et al. 2001), which are both *not* part of the posterior cortex, and that these representations are reactivated when the motor information is retrieved (Heil et al. 1999). Similarly, the premotor cortex is also activated when manipulable objects, as opposed to non-manipulable ones, are maintained in working memory (Mecklinger et al. 2002). Recent evidence also shows that over anterior scalp areas different event-related potential (ERP) topographies are evoked, if either verbs or nouns are accessed (Khader et al. 2003). Finally, the role of the left frontal cortex (certainly not a part of the posterior cortex) in the representation of verbal and/or semantic information in both short-term and long-term memory tasks cannot be underestimated (see, e.g., Heil et al. 1996; Paulesu et al. 1993). To sum all this up, the idea that memory representations are restricted to the posterior cortex does not survive empirical tests – leaving aside the fact that Ruchkin et al. don't even specify what the "posterior" cortex does actually embrace.

Control and maintenance of activation in memory are assumed by Ruchkin et al. to be done by the prefrontal cortex. Although there is support for this idea regarding the function of the prefrontal cortex, the data, in fact, suggest a domain-specific regional organization of the prefrontal cortex (e.g., Goldman-Rakic et al. 2000). Because of the limits in the spatial power of the EEG, however, Ruchkin et al.'s own data do not address this point satisfactorily. Therefore, this assumption of Ruchkin et al. remains quite nebulous. Fortunately, other elaborated models based on high-quality data (e.g., D'Esposito et al. 2000) already exist showing that the prefrontal cortex is not a functionally unitary entity.

The idea of a hippocampal contribution, or more generally, subcortical contributions to memory, is ignored. It is quite obvious that a theory of memory has to incorporate the contribution of the hippocampus (see, e.g., Squire 1992). O'Reilly and Norman (2002), for example, present a complementary framework for the hippocampal and the neocortical contributions to memory. And, of course, memory functions critically depend on additional subcortical structures, even if one were to ignore the emotional embedding of information (see, e.g., Markowitsch 2000). It is true that the EEG has a somewhat blind spot for the neural activity in subcortical structures, but that does not justify the theory itself suffering from that same shortcoming.

So what is left of the theory proposed by Ruchkin et al. is (1) the idea that short-term memory should be understood as the active part of long-term memory, (2) the idea that content-specific representations in the neocortex are activated when information is processed, stored, and retrieved, and (3) the idea that the prefrontal cortex plays an important role in some kind of control of activation. In fact, none of this is new (see, e.g., Rösler & Heil 2003, for an overview of existing theories). The artificial division between posterior cortical areas that do represent information and prefrontal cortical areas that do not represent information is new, at best, but should not be adopted in cognitive neuroscience as long as no more convincing data are presented.

Temporal lobe speech perception systems are part of the verbal working memory circuit: Evidence from two recent fMRI studies

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Abstract: In the verbal domain, there is only very weak evidence favoring the view that working memory is an active state of long-term memory. We strengthen existing evidence by reviewing two recent fMRI studies of verbal working memory, which clearly demonstrate activation in the superior temporal lobe, a region known to be involved in processing speech during comprehension tasks.

The argument favoring the hypothesis, that working memory is an active state of long-term memory, is relatively weak in the verbal domain. The weakness stems from the following observation: Fronto-parietal areas have been implicated in verbal working memory, both in previous hemodynamic imaging studies (Smith & Jonides 1997) and in the current article, yet these areas are not implicated in the auditory perception/comprehension of verbal material. For example, studies of passive listening to speech stimuli – which no doubt activate long-term memories (and/or perceptual processing systems) for verbal material – have implicated superior temporal regions bilaterally, not frontal or parietal cortices (Hickok & Poeppel 2000). Lesion evidence similarly implicates the superior and middle temporal gyri in the perception and comprehension of speech (Dronkers et al. 2000; Hickok & Poeppel 2000). If verbal working memory is an active state of systems involved in representing/processing speech, we expect the supe-

rior temporal lobe to be regularly implicated in auditory verbal working memory, yet it is not.

Two recent fMRI studies conducted in our lab resolve this apparent contradiction. These studies used a novel paradigm, in which, on each trial, subjects were presented with acoustic speech information, which they then rehearsed subvocally for an extended period of time (15 to 27 seconds in different experiments), followed by a rest period. Analysis focused on identifying regions that were responsive *both* during the perceptual phase and the rehearsal phase of the trial. The logic of this design was driven by several factors, one of which was the behavioral demonstration that irrelevant acoustic information interferes with immediate serial recall (the irrelevant speech/sound effect, Jones & Macken 1996; Salamé & Baddeley 1982), suggesting that acoustic information has obligatory access to short-term storage systems. From a neurophysiological standpoint, this means that a region supporting short-term storage should be responsive not only to maintenance of acoustic information, but also to the simple perceptual presentation of that information (Becker et al. 1999), hence the focus on regions with combined perceptual + rehearsal response properties.

Using this technique, and in two separate studies (Buchsbaum et al. 2001; Hickok et al. 2003), we identified a network of regions with these response properties. This network included two frontal regions, Broca's area and a premotor site, consistent with previous studies (Smith & Jonides 1997), and thought to be involved in articulatory rehearsal. But relevant to the present discussion, we also found two locations in the superior temporal lobe, one in the superior temporal sulcus (STS) bilaterally, and one along the dorsal surface of the left posterior superior temporal gyrus, that is, in the Sylvian fissure at the parietal-temporal boundary (an area we have called Spt). Figure 1 presents a group-averaged activation map from a meta-analysis of these two studies, showing the temporal lobe activation sites (as well as the frontal activation). The STS locations (bilaterally) clearly map onto regions that have been implicated in auditory speech perception/comprehension (Hickok & Poeppel 2000), thus providing strong support for the hypothesis that verbal working memory is an active state of more fundamental processing/representation systems. Nonlinguistic auditory stimuli (music) produce a very similar activation pattern in the same task (Hickok et al. 2003), suggesting that this network is not linguistic-specific; a result consistent with behavioral data (Jones & Macken 1996). Previous studies may have missed these temporal lobe activations: (1) because of anatomical variability in this region leading to partial averaging effects, (2) because subtraction conditions involved acoustic controls, or (3) in the case of the electrophysiological work, because the activity buried in a deep fissure and possibly on opposite banks of that fissure, may not be visible to EEG methods.

Although the STS activations are consistent with sites involved in perception/comprehension of speech, the functional role of the parietal-temporal activation (area Spt) is less obvious. Damage to

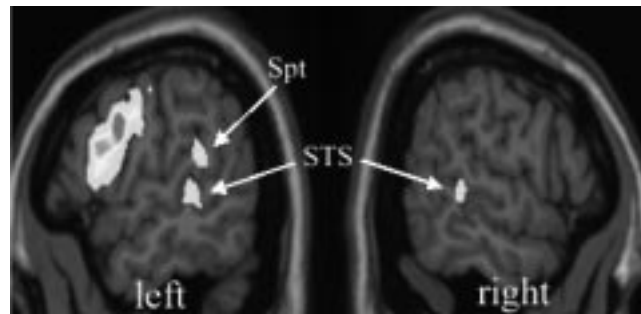


Figure 1 (Hickok & Buchsbaum). Cortical regions showing fMRI activation both during the auditory perceptual and (covert) rehearsal phases of a verbal short-term memory task (pooled data from 10 participants).

this region does not produce speech perception or comprehension deficits, but it has been implicated separately in short-term verbal memory deficits (Shallice & Vallar 1990) and in conduction aphasia (Damasio & Damasio 1980; Hickok 2000; Hickok et al. 2003). We have hypothesized (Hickok et al. 2003; Hickok & Poeppel 2000) that area Spt represents a kind of interface network, performing a computation (see, e.g., Guenther et al. 1998) that transforms between auditory-based representations of speech in the lateral temporal lobe (STS) and articulatory-based representations in frontal cortex. Such a network is critical in development, as the mechanism allowing acoustic speech input to guide the tuning of articulator gestures appropriate to the phonetic patterns of the language being acquired (Doupe & Kuhl 1999), and aspects of normal speech production (Buchsbaum et al. 2001), and once established, could be coopted for short-term memory tasks. According to this view, verbal working memory (and perhaps working memory in general) can be explained in terms of more basic sensory-motor loops (Wilson 2001), the activation of which is presumably triggered by some sort of executive mechanism, as discussed in the target article.

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What is the source of activation for working memory?

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Abstract: Attentional processes that operate on the contents of memory to produce the activation that is described as working memory by Ruchkin et al. and others, involve a network of brain regions that include both prefrontal and parietal sites. This network appears to mimic the one that is activated by attentional processes that operate on information entering via the senses.

Let us assume that working memory is a function of activated representations in long-term memory, as presented by Ruchkin et al. in the target article. What are the brain mechanisms that mediate this activation? There is sufficient evidence to implicate not only frontal cortex but posterior, superior parietal cortex, as well.

Consider first, spatial working memory. Various studies implicate a rehearsal mechanism needed to keep spatial information activated during a retention interval. The first researchers to document the mechanisms involved in spatial working memory in humans were Jonides et al. (1993), who showed that there was substantial activation in extrastriate and superior posterior parietal cortex, in addition to activation in frontal cortex. Others have also shown similar patterns of activation, in addition to documenting the engagement of superior frontal mechanisms (e.g., Courtney et al. 1998). Awh et al. (1999) accumulated evidence from behavioral and imaging studies suggesting that activation in extrastriate cortex is modulated during the rehearsal of information in spatial working memory. What modulates the activation of this site appears to be control signals from the superior parietal lobule and intraparietal sulcus, the very same regions that have now been documented as some of the sources of control when people attend to visual stimuli (e.g., Kastner & Ungerleider 2000). So, research on spatial working memory implicates a network of frontal and parietal mechanisms in the activation of memory representations.

Consider next, working memory for objects. There is evidence of a common mechanism involved in attending to objects and maintaining objects in working memory. Downing (2000) has shown that when an object is held in working memory, attention is diverted to that object if it appears in a visual display. Also, Pash-

ler and Shiu (1999) have shown that having an object in mind causes attention to be called to that object if it appears in a visual array. These data raise the possibility that the mechanism that supports activation of an object's representation in working memory may be the same as the mechanism that causes attention to be shifted to an object in the visual world. Serences et al. (in preparation) have shown that this mechanism of object-based attention involves a combination of frontal and parietal regions, with the parietal regions being similar to those involved in the allocation of attention to spatial locations. Earlier, Smith et al. (1995) had shown that retention of objects in working memory also activated a parietal region, as well. Taken together, these reports lead to the view that object working memory may also make use of activation mechanisms of frontal and parietal cortex.

Finally, let us examine verbal working memory. There is ample evidence that rehearsal contributes to the maintenance of information in verbal working memory. How does rehearsal work? Naveh-Benjamin and Jonides (1984) showed that early during rehearsal, attention is needed, possibly to set up the sequence of phonological representations that are cycled. Later on during rehearsal, the cycling of representations is more automated. These results implicate an attentional process, in at least the early portions of a retention interval, during which attention is shifted from one representation to another as a rehearsal loop is constructed. This cycling of attention is, by hypothesis, in the service of setting up phonological codes that represent the items that are being rehearsed.

So, a behavioral analysis of rehearsal implicates two sorts of processes, one tied to the form of information that is stored (language-like) and one tied to an attentional system that is needed to create a rehearsal loop. Evidence from neuroimaging studies of verbal working memory clarify which brain systems are recruited for these two components. Rehearsal relies on structures in the inferior frontal gyrus and premotor cortex associated with language production (Awh et al. 1996). These are presumably activated because it is phonological (and possibly other language-like) representations that are being maintained in verbal working memory. This is not all there is to the circuit, however. We and other researchers have isolated rehearsal during verbal working memory and found activation, not only of the inferior frontal gyrus and premotor cortex, but also superior aspects of the posterior parietal cortex and medial frontal cortex (SMA/ACC) (Smith & Jonides 1997). The SMA/ACC activation has often been associated with an attentional circuit (Posner & Petersen 1990), and the superior parietal lobule and intraparietal sulcus are also key elements in allocating and switching attention (Yantis & Serences 2003). Indeed, two meta-analyses, one of attention (Kastner & Ungerleider 2000) and one of the switching of attention (Wager & Jonides, in preparation), show that these regions of posterior parietal cortex are critical to the engagement and disengagement of attention. Added to evidence from patients (Posner et al. 1984) and from single unit studies of monkeys (e.g., Bisley & Goldberg 2003; di Pellegrino & Wise 1993), it appears that the source of attentional modulation is a combination of frontal (including SMA/ACC, but also perhaps frontal eye fields) and parietal mechanisms working in concert.

So, what is it that we know from this evidence about working memory for different kinds of information? First, we know that rehearsal is an integral process, no matter what the type of material. Beyond this, we know a good deal about a common neural substrate that appears to be involved in rehearsal, regardless of the type of material. The participating brain regions are similar to those that control attention in the visual world, whether to spatial properties, object properties, or even task properties (Wager & Jonides, in preparation). This circuitry involves not only frontal control, as Ruchkin et al. argue, but also parietal control. It is not at all clear how the frontal and parietal mechanisms work together, although it is clear that they are highly interconnected (Petrides & Pandya 1984) in a reciprocal fashion. It is interesting to note that this is one more occasion on which a mechanism, presumably

evolved for the control of perceptual processing, has been adopted for the processing of internal representations, perhaps a theme common to other kinds of higher-order cognitive processes as well.

Incorporating semantics and individual differences in models of working memory

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Abstract: Ruchkin et al.'s view of working memory as activated long-term memory is more compatible with language processing than models such as Baddeley's, but it raises questions about individual differences in working memory and the validity of domain-general capacity estimates. Does it make sense to refer to someone as having low working memory capacity if capacity depends on particular knowledge structures tapped by the task?

The target article by Ruchkin et al. is an excellent demonstration of how cognitive neuroscience can help solve key theoretical controversies in cognitive psychology. The debate over whether short-term or working memory and long-term memory represent different states of a single system or two distinct memory systems has a long history. The event-related potential (ERP) findings of Ruchkin et al. provide strong support for the view that working memory is the activation of relevant long-term memory representations (cf. Cowan 1988). At the same time, however, they also corroborate the two-systems view (e.g., Baddeley 1986), in that the activated long-term memory representations of posterior cortex are separate from the prefrontal cortical system that maintains the activations. Thus, both sides of the debate are shown to have merit.

One particularly appealing feature of the present formulation is that it accommodates lexical and semantic working-memory systems. Anyone who studies discourse processing realizes the need for a semantic working memory to allow meanings of earlier parts of a discourse to be integrated with later parts. Although the phonological loop of Baddeley's (1986) working memory has been posited as the basis for such integration, it is more parsimonious to have the means for sustaining activation be through the semantic, rather than the phonological, system because the integration is across semantic representations. Not only does it make sense that there is a semantic working memory for language processing, but there are data which are hard to explain without it. One type of such data is the performance of patients with profound phonological memory deficits on sentence repetition tasks; even though their phonological deficit prevents them from repeating the sentence back in its exact wording, they can repeat its meaning, suggesting the existence of a semantic working memory (Martin et al. 1994). Perhaps if language comprehension, rather than span tasks, had been the target behavior in studies of working memory, the status of semantics in models of working memory, such as Baddeley's (1986), would have been greater. Certainly, findings such as Ruchkin et al.'s that lexical-semantic codes interact throughout the retention interval, as opposed to only during retrieval, will play an important role in opening the door to a view of working memory that is more inclusive of semantic processes.

One very important issue that remains unresolved is the nature of individual differences in working-memory capacity. The long-standing tradition, exemplified by span measures of working-memory capacity, is that individuals possess a domain-general storage or storage/processing system whose capacity is measured

by span tasks and is independent of the type of knowledge being maintained. Ruchkin et al.'s view that working memory is the activation of relevant long-term memory representations raises questions about the validity of domain-general capacity estimates. Does it make sense to refer to someone as having high or low working-memory capacity if the capacity of one's working memory depends on particular knowledge structures tapped by the task (cf. Ericsson & Kintsch 1995)?

The notion that the capacity of working memory depends on the knowledge domain assessed by the task was first demonstrated by Chase and Ericsson (1982). After a year of practicing digit span, their subject, SF, learned to expand his span from 7 to 84 digits; importantly, the practice had no effect on his span for letters or words. Outside the realm of span tasks, our own research has shown the importance of knowledge structures in the capacity of working memory. One study examined reader's eye fixations as they read texts from a designated encoding perspective, making some information relevant and some irrelevant to the perspective (Kaakinen et al. 2003). Eye fixation durations reflect working memory in that the more easily the fixated information can be integrated with information in working memory, the shorter the fixation time. Previous work established that readers always remember relevant information better than irrelevant information; the question we asked is whether that is because relevant information gets fixated longer. We found that whether this differential memory for relevant information is accompanied by differential encoding times depends on the familiarity of the text's content. Relevant information tends to be fixated longer than irrelevant information, unless it is highly familiar. For highly familiar information, readers were able to encode relevant information without incurring time-consuming processing. This finding clearly supports the notion that differences in knowledge structures underlie differences in working memory. However, there is one hitch to this. We classified readers as having high or low working-memory capacity, depending on their performance on a reading-span task (Daneman & Carpenter 1980). It was only the high-span readers that showed the interaction with familiarity and perspective relevance. Low-capacity readers needed extra encoding time to achieve the same end result. This finding indicates that individual differences in working-memory capacity may not only be a result of differential knowledge, but also may result from differential ability to make use of that knowledge.

Our results suggest that individual differences in working memory may derive from two sources. One is, individual differences in the knowledge structures of the posterior cortical systems. The other may be individual differences in the resources of the prefrontal cortical system that keeps these knowledge structures activated. It is important to note, however, that these two systems may not be that independent. It could be that posterior cortical knowledge representations that are more interconnected or have stronger links may be easier to keep activated. Or, in terms of our experiment, people who do well on a reading-span task are people who are capable of fast and easy access to LTM representations; and in fact, that's why they do well on the reading-span task. In other words, using existing LTM representations, they are able to quickly create semantic connections between the to-be-remembered information.

Ruchkin et al. have done much to move the working-memory field beyond the one- versus two-memory systems debate. It is our hope that future studies using this ERP methodology will also help to clarify whether the nature of individual differences lies in the number of pointers active in the prefrontal cortex, or in the ease, speed, and breadth of activating posterior brain areas that are assumed to be responsible for long-term memory representations, or both.

Activation of long-term memory by alpha oscillations in a working-memory task?

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Abstract: We focus on the functional specificity of theta and alpha oscillations and show that theta is related to working memory, whereas alpha is related to semantic long-term memory. Recent studies, however, indicate that alpha oscillations also play an important role during short-term memory retention and retrieval. This latter finding provides support for the basic hypothesis suggested by Ruchkin et al.

We consider four typical findings. (1) Theta oscillations (with a frequency of about 6 Hz) reflect working memory, and (2) upper alpha (with a frequency of about 12 Hz) reflect semantic long-term memory. (3) Increased working-memory load during retention is reflected by increased theta activity over frontal areas and by (4) increased upper alpha activity over parietal regions that are associated with short-term memory storage. Our argument is that the load-dependent increase in upper alpha activity during retention may reflect the activation of long-term memory structures.

Although it has been questioned for a long time, there is still convincing evidence that theta oscillations can also be observed in humans, and that an increase in theta reflects working-memory demands (for an extensive review, see Klimesch 1999). There is also evidence that the topography of theta activity is associated with those cortical regions that are known to play an important role in working memory. As an example, Sarnthein et al. (1998) have found a significant increase in long-range theta coherence between prefrontal and posterior electrodes during a short-term retention task (as compared to a control task). In the verbal task, the pattern of coherent theta oscillations showed a network connecting left occipito-temporal with bilateral prefrontal regions. In the visual task, a more bilateral pattern was observed. The general interpretation of these and similar findings (Anokhin et al. 1999) is that theta oscillations reflect (at least some of those) neural processes that are relevant for working memory, comprising central executive processes located in frontal areas and coordination with short-term storage processes located in parietal areas (Baddeley 2000).

Alpha oscillations show a strikingly different pattern of physiological and functional reactivity. In contrast to theta, alpha oscillations decrease (desynchronize) with (sensory-semantic) task demands. Studies from our laboratory and other investigators indicate that the upper alpha frequency range (of about 10–12 Hz) responds selectively to sensory-semantic memory processes of a complex long-term memory system (cf. Klimesch 1999 for an extensive review). As a more recent example, let us briefly review findings from a sentence-processing task (Röhm et al. 2001). Sentences (such as “A rabbit is in the box, hiding”) were presented in four chunks under two task conditions, a reading task and a semantic task. Whereas in the first task, subjects simply had to read the sentences, in the second (semantic) task an additional, semantic process had to be carried out. Subjects were instructed to find the superordinate concept to the noun of the third chunk (which is “container” in response to “box” in the present example). The findings indicate that, for the theta band, the event-related increase in band power is largest during processing of the first chunk and smallest for the fourth chunk. This seems to indicate that processing demands for working memory are largest during the processing of the first chunk (when subjects are prepared to encode the next following chunks) and lowest for the fourth chunk, when all parts can be successfully integrated into a sentence. The opposite pattern of results was obtained for the upper alpha band. Here, the extent of decrease in band power (desyn-

chronization) was largest in the semantic task during the retrieval of the superordinate concept. Thus, the findings suggest that retrieving a superordinate concept from semantic memory is a process that does not draw on the capacity of the working-memory system.

For the retention period of memory-scanning tasks (such as the Sternberg and n-back task), an interesting similarity between the reactivity of theta and upper alpha oscillations, with respect to memory load, was found. Whereas it is well established that theta power increases with load (e.g., Gevins & Smith 2000; Jensen & Tesche 2002), several recent studies have found similar effects in the alpha frequency range, although with a different topography (Jensen et al. 2002; Klimesch et al. 1999; Schack & Klimesch 2002). These latter findings are surprising because it is so well documented that alpha power decreases with task demands.

In a recent study (Schack & Klimesch 2002), we have analyzed this phenomenon of paradoxical alpha synchronization in a Sternberg task with number words. We found that upper alpha power (at 12 Hz) increased significantly with set size at posterior recording sites (particularly at Pz and P4) during retention. Most interestingly, during retrieval, exactly within that frequency range, a significant increase in evoked power at 12 Hz could be observed, even in the event-related potential (ERP). In addition, we found that the extent of phase locking in upper alpha increased with set size. These findings indicate that oscillatory EEG activity in peak alpha frequency (functionally associated with the maintenance of information in working memory during retention) is related to evoked activity and increased phase locking during retrieval and memory scanning. Furthermore, the P3b (at Pz and P4) coincides with the last of three evoked alpha peaks. Thus, these findings strongly suggest that alpha oscillations play an active role in working memory, not only during retention but during scanning and retrieval as well. The latter finding implies that alpha oscillations coordinate the encoding of the probe, the scanning process, and the evaluation of the read-out process, which most likely is manifested by the P3b. When considering the functional specificity of alpha for semantic long-term memory and the topography of alpha phase locking and evoked activity over parietal areas, we may conclude that phase-locked alpha during scanning and retrieval reflects the “coactivation” of storage networks in long-term memory (LTM) where numbers are presented.

Retention systems of the brain: Evidence from neuropsychological patients

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Abstract: Studies of neuropsychological patients are relevant to models of how long-term memories are stored. If amnesia is considered a binding deficit and not a difficulty in transferring information from short-term to long-term memory, it is unclear why context-free semantic learning is impaired. Also the model should account for the reverse temporal gradient seen in patients with semantic dementia.

The dissociation of short-term and long-term memory abilities in amnesic patients is considered one of the most important findings supporting the idea that there are separate stores. However, Ruchkin et al. note that this dissociation could be accounted for if one assumes that the deficit in amnesia is one of binding rather than the formation of long-term memory representations. By this view, there are no differences between the long-term memory representations in amnesic patients and neurologically intact individuals. Although amnesic patients are able to dynamically bind representations in working memory, they are impaired at the formation of bindings between the elements of a memory that support its long-term retrieval. According to this view, the brain struc-

tures damaged in amnesia (e.g., medial temporal lobe structures) play a role in forging these new bindings between preexisting elements in long-term memory.

The idea that amnesia is a deficit in long-term binding is appealing. Patients with amnesia exhibit severe deficits in episodic memory, or memory for experienced events. Fundamental to the definition of episodic memories is the idea that they are comprised of disparate temporal and contextual (external and internal) elements that uniquely determine each episode. If amnesic patients were unable to bind these elements in the long term, they would exhibit impaired retention of episodes once they are no longer held in working memory. However, amnesic patients, particularly those in whom medial temporal lobe damage extends outside of the hippocampus, are also impaired at learning new semantic information, such as facts and new vocabulary words (Squire & Zola 1998). They also exhibit impaired memory based on familiarity (Yonelinas et al. 1998). For these types of memory it is not clear how formation of semantic memories depends on long-term binding. Learning a new vocabulary word could be viewed as forming new connections between the phonological elements of the word and semantic elements. However, it is not obvious why amnesic patients would be impaired at this type of binding, but not the type of binding that supports non-declarative forms of learning that are intact in amnesia, such as priming for novel information, text-specific facilitation of reading speed with practice, and sequence-specific learning in the serial reaction time task (Squire et al. 1993). It may be that amnesic patients are specifically impaired in binding that leads to consciously accessible (or declarative) information. However, it seems somewhat more parsimonious to hypothesize that they are impaired at the formation of declarative memory representations, rather than in a particular set of binding processes.

In addition to studies of amnesia, equally important insights into memory function have been gained by research on how depth-of-processing manipulations facilitate later memory retrieval (Craik & Lockhart 1972). If one hypothesizes that the encoding of new memories results in the creation of new representations, one would suppose that deep, semantic encoding of information would create a richer, more interconnected, and more robust memory representation than when only surface features are processed. However, if one views the creation of new memories as the formation of new bindings between pre-existing elements, one would interpret deeper encoding as leading to more extensive binding. However, one might predict that if amnesic patients have deficient long-term binding processes, they would not benefit as much as neurologically intact individuals would from deeper processing at study. In fact, depth-of-processing effects are generally proportional for amnesic patients (Hamann & Squire 1996), suggesting that amnesia and depth of processing affect memory independently.

Another neuropsychological syndrome that is relevant to the study of memory representations is semantic dementia. Semantic dementia (SD) is a clinical term given to the temporal variant of frontotemporal dementia in which the affected patient shows progressive focal atrophy of the inferolateral aspect of the left and/or right temporal lobes with (in the early stages) relative sparing of the hippocampal complex (Graham & Hodges 1997). Although SD patients show a severe loss of semantic information (i.e., picture naming, verbal definitions of words, category fluency) and produce errors that reflect a loss of subordinate information while having superordinate information relatively preserved, they are able to recall recent life events with relative clarity and often perform relatively well on tests of nonverbal working memory (Hodges & Miller 2001). Patients with SD have also been found to show a temporal gradient in recognition of famous people that is the reverse of that shown by amnesic patients. Hodges and Graham (1998) reported that four patients with semantic dementia were better able to recognize currently famous individuals than previously famous individuals from a set of names of famous and nonfamous people. They were also better at identifying informa-

tion about currently famous people. These results provide compelling evidence that individuals with lateral temporal damage are able to store memories, initially, in a part of the brain (presumably the medial temporal lobes) that remains intact. Older knowledge, perhaps because it has been relocated to regions that are damaged by the disease process, does not fare as well. If long-term memories are simply bound representations of pre-existing knowledge, it is unclear why recent memories are spared if they depend on the same set of stored representations as more remote memories. It would seem that new memories and older memories should be equally affected by a loss of semantic knowledge. Rather, these data seem more consistent with the idea that recent memories depend on different neural representations than older memories. If memory representations depend on different neural substrates as they age, and if working memory is simply activation of long-term memory, this raises the question of how "activated" recent and remote memories may differ.

Ruchkin et al. have made a compelling case for their view based on electrophysiological and behavioral evidence from neurologically intact individuals. It is important to account for the data from neuropsychological patients, as well. It may be that their model can be made consistent with neuropsychological findings, if certain assumptions are made as to the processes impaired in these patients. Hopefully, these assumptions will be testable as a means to further assess their model.

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Long-term memories, features, and novelty

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Abstract: Ruchkin et al. make a strong claim about the neural substrates of active information. Some qualifications on that conclusion are: (1) Long-term memories and neural substrates activated for perception of information are not the same thing; (2) humans are capable of retaining novel information in working memory, which is not long-term memory; (3) the content of working memory, a dynamically bound representation, is a quantity above and beyond the long-term memories activated, or the activity in perceptual substrates.

Ruchkin et al. present compelling evidence that information in working memory, rather than existing in a special purpose buffer distinct from the neural substrates specialized for perceiving that kind of information, is a state of activation in those same substrates under the control of frontal cortex. As the authors note, this is a more parsimonious scheme than duplicate representation architectures for the perception and storage of the myriad kinds of information we deal with. The view that attention activates representations, even in low-level visual areas, has also been demonstrated for nonverbal information by Kastner et al. (1999) and others, and the control of posterior representations by frontal cortex was embodied in our computational model of working memory (Kroger et al. 1998).

It might be possible to make a more explicit distinction between "long-term memory" in the sense of semantic information that is activated (e.g., in inferior temporal cortex) during retention of verbal information in working memory, and the neural substrates that are engaged as information is perceived. In terms of verbal information, there may be a great deal of overlap, as perceived words typically activate areas specific to semantic information storage. However, as a general principle of information storage, some caution is called for. It is well established that cells in primary visual

cortex participate in perception of light and dark, orientation, and so on. Although it seems straightforward that retaining information in working memory about a fixation dot, or the location of a saccade target, may involve activation of regions that participated in its perception, it is less clear that this is an activated long-term memory. Suppose subjects are presented with a novel shape to remember. It could be argued that elements of the shape (corners, curves, etc.) are retained by invoking neural representations of these features learned over time, thus perhaps constituting long-term memories bound in the current episode into the novel shape. In the case of five novel shapes, of different colors, the argument could be similarly made that the content of working memory is a binding of long-term memories. It seems, however, that there is a meaningful sense in which the “content” of working memory is more a binding of features to constitute a new representation than it is activated long-term memories. In the same vein, the proposition “John loves Mary” is distinct from the proposition “Mary loves John,” although the same long-term memory elements may be activated by both. What if one has never met John, does not know which John is being referred to, or has never encountered the name “John” before? The degree to which the content of working memory includes activated long-term memory varies, and semantic and episodic associations activated along with the proposition may vary, but the simple proposition “John loves Mary” can exist in working memory apart from this extra information. As with novel shapes, it may be argued that novel information is retained that does not depend on long-term memories.

The relocation of working memory content from separate buffers, as proposed by Baddeley (1986), to the neural substrates specialized for perception of information is an important and necessary step that will help enable the study of how frontal cortex and attention accomplish that which Ruchkin and his coauthors term “episodic” bindings. Now that neuroimaging methods permit observation of the actual substrates of memory retention, the notion that separate regions exist for buffering and for perception of information could interfere with proper interpretations of neuroimaging results, and is no longer tenable. This is especially true because these buffers were often associated with frontal activity observed during retention, which more likely is involved in attentional control of working memory, as the authors suggest. Long-term memory may become activated as meaningful stimuli, such as words, are retained in working memory, but it is important to remember that humans are facile at retaining novel information, and novel, complex bindings of information. In these instances, the nature of “what is in working memory” transcends the collection of activated perceptual substrates or long-term memories that may be active, especially in the context of research on higher cognition.

Some neuroimaging results suggest that, as the representations bound together in working memory increase in complexity, but not as memory load increases, more anterior regions of prefrontal cortex are recruited (Kroger et al. 2002).

Working memory as a mental workspace: Why activated long-term memory is not enough

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Abstract: Working-memory retention as activated long-term memory fails to capture orchestrated processing and storage, the hallmark of the concept of working memory. The event-related potential (ERP) data are compatible with working memory as a mental workspace that holds and manipulates information on line, which is distinct from long-term memory, and deals with the products of activated traces from stored knowledge.

Ruchkin et al. equate working-memory retention systems with short-term memory. One advantage of the multiple-component working-memory concept is that it incorporates both on-line processing and temporary memory (e.g., Baddeley & Logie 1999), allowing the concept of working memory as a mental workspace (Logie 1995), rather than as a simple temporary storage device. The notion of working memory retention systems as comprising a state of activated long-term memory fails to capture, or to account for, this concept of orchestrated processing plus storage. A multiple-component working memory, as a mental workspace that is separate from, but holds and manipulates the products of activated traces in long-term memory (Logie 1995; 2003), retains the advantages of offering a testable theory, while accounting for a wide range of behavioural data, both from experimental manipulations and from neuropsychological dissociations (Della Sala & Logie 2002).

Ruchkin et al. argue that it is more parsimonious to assume that short-term memory reflects simply the activation of long-term memory traces, than to assume a separate, multiple-component working-memory system. However, the former theory has to make a wide range of assumptions regarding: the operation of the activation process, how thresholds are set or adjusted, how non-relevant but activated traces are inhibited, how the temporary binding process occurs and is maintained with input from different modalities, how the activated information is manipulated (anything from backward digit recall to generating novel mental images), and how the novel results of those manipulations are held on a temporary basis (for detailed discussion, see Logie 2003). Moreover, a model that explains dual-task interference in terms of similarity of the codes used for each task sounds dangerously circular. Suggesting that two tasks interfere because they use similar codes has some difficulty in making predictions independently of the experimental outcome (Cocchini et al. 2002). In other words, assuming that working-memory retention systems and long-term memory arise from the same conceptual cognitive systems may well be theoretically sterile.

One feature of experimental research into human cognition that is all too rarely recognised is the use of a range of cognitive strategies by participants. Logie et al. (1996) demonstrated that even very simple immediate serial-ordered recall tasks are prone to the use of a range of cognitive strategies, both across individuals, and within the same individual from one occasion to another, even if the aggregate data for the sample of participants generate reliable behavioural phenomena. Indeed, some fMRI data of our own (Logie et al., in press) have shown that specifically instructing participants to use subvocal rehearsal results in a relatively narrow range of areas of activation, focused on Broca's area and the supramarginal gyrus, compared with the much broader network of activation patterns, including those same areas, reported by Paulesu et al. (1993). Interpreting precisely what kind of cognitive function might be employed for any given task requires a very careful cognitive-task analysis, with independent behavioural evidence to indicate precisely how participants are performing the tasks. Without this, at best, the activation patterns can be seen as correlates of how, on average, the participant group performed the task they were set. This is not necessarily informative about the cognitive systems that participants may select to meet the requirements of the task in hand. This kind of detailed cognitive-task analysis is not common in brain imaging studies, and this makes it very difficult to suggest that a given aggregate pattern of activation is reflecting any particular cognitive function. The result may then be a mapping of tasks onto brain structures rather than a mapping of cognitive functions onto brain organisation. In this sense, brain activation patterns might be used to confirm a cognitive theory, but they need not constrain that theory.

The bulk of the evidence described by Ruchkin et al. focuses on the argument that activation of the same brain areas indicates that the same cognitive function is involved. Specifically, because the same brain areas are active for tasks that are assumed to require temporary retention as are involved in activation of stored knowl-

edge or of previous episodes, then there is no need to postulate separate short-term and long-term memory systems. However, different time courses of the task result in different time courses of the ERP trace, a result that could reflect different modes of operation (and hence, functionally different cognitive functions) of the same brain structures. Moreover, maintenance of material on a temporary basis, beyond the end of stimulus presentation, is associated with activity in the prefrontal areas, as well as in the posterior areas, which have been linked to activation of long-term memory. As Ruchkin et al. point out, the advantage of word lists over nonword lists in immediate serial- and free-recall tasks indicates an involvement of semantic information in supporting temporary memory functions. However, there is nothing in the reported ERP data that constrains the interpretation that temporary retention involves areas of the prefrontal cortex, in addition to some form of ongoing activation of the recently activated traces in long-term memory. Temporary memory appears to be associated with both anterior and posterior areas of activation. This could suggest that the prefrontal cortex is the seat of temporary memory, or that both the prefrontal and the posterior activation are required in such tasks, or that the prefrontal activation reflects the operation of some form of controlling mechanism that ensures continued maintenance of long-term memory traces. In all cases, there is a different network of activation associated with temporary memory than with long-term memory tasks, even if there is some overlap in the brain areas involved. At a conceptual level, all three of these interpretations are quite consistent with working memory holding the products of activated traces from long-term memory; they are also consistent with working memory comprising a system that is conceptually quite distinct from long-term memory.

Does sustained ERP activity in posterior lexico-semantic processing areas during short-term memory tasks only reflect activated long-term memory?

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Abstract: We challenge Ruchkin et al.'s claim in reducing short-term memory (STM) to the active part of long-term memory (LTM), by showing that their data cannot rule out the possibility that activation of posterior brain regions could also reflect the contribution of a verbal STM buffer.

Ruchkin et al. argue that they provide strong evidence for a lexico-semantic contribution to verbal short-term memory (STM) tasks, by showing greater event-related potential (ERP) activity in posterior lexico-semantic processing areas (most pronounced in the vicinity of the central midline scalp) during the retention of STM lists of five words compared to STM lists of three nonwords. At an empirical level, we support Ruchkin et al.'s results, as we also observed very similar data in a recent positron emission tomography (PET) study investigating lexicality effects in STM. Collette et al. (2001) explored the activation of posterior brain areas in both a STM task (ordered recall of three words vs. three nonwords) and a control condition (repetition of one word vs. one nonword). When comparing brain regions activated for words versus nonwords in the STM condition, after accounting for brain regions already activated when contrasting words and nonwords in the control condition, we observed greater activation in two posterior

brain regions, the left middle temporal gyrus (BA 21) and the left temporo-parietal junction (BA 39). Our data clearly support the idea that posterior brain areas play an active role during short-term retention of words and further complement the data of Ruchkin et al. by providing a more precise localization of these brain regions.

However, at a theoretical level, we consider that there might be an alternative interpretation for the activation of posterior brain regions during STM processing of words than the interpretation put forward by Ruchkin et al. They consider that their data support the position that STM mainly reflects the activated state of LTM, based on similar activation of posterior brain areas thought to encode lexico-semantic language knowledge during both single-word processing and STM for words, relative to single-nonword processing and STM for nonwords. This interpretation includes the implicit assumption that the observed activation of posterior processing areas exclusively reflects the neural substrate of lexico-semantic representations encoded in LTM. However, we think that the results cannot exclude the possibility that the posterior brain areas activated in that study could also reflect the contribution of a STM buffer in addition to activation of lexico-semantic knowledge in LTM. First, the posterior regions encoding lexico-semantic knowledge and those having a buffer function, although different, could be spatially very close and thus difficult to distinguish by ERP techniques, which have a relatively poor spatial resolution. Second, the authors compared recall of five words versus three nonwords in order to achieve a similar level of STM performance for words and nonwords. However, a similar level of performance does not guarantee that the requirements of STM storage capacities are the same in both tasks; it is still possible that STM load was greater in the word than in the nonword condition, especially as the words (five items) had to be maintained longer in STM than the nonwords (three items) before recall. By extension, this implies that the greater ERP activation observed in posterior brain regions during STM for words relative to nonwords could also reflect the activation of a STM buffer, and not only activation of lexico-semantic knowledge as proposed by the authors. Third, we recently showed more directly that posterior brain regions could have a specific STM buffer function for verbal information, by studying brain activation using PET imaging for verbal STM performance in three patients that had recovered from Landau-Kleffner syndrome, a rare epileptic childhood aphasia characterized by persistent verbal STM impairments (Majerus et al. 2003a). The patients were presented lists of four words for immediate serial recall and a control condition (repetition of one word); there was also a control group of 14 healthy young adults. Two of the patients showed reduced activation in left and right posterior superior temporo-parietal areas during the STM condition compared to the control condition, and they presented, at the same time, impaired performance in the STM condition. The third patient showed increased activation in the right posterior superior temporo-parietal area in the STM condition, while presenting, at the same time, relatively normal STM performance. These results suggest that activation of the posterior temporo-parietal area determines very directly the level of performance observed in the STM condition. Furthermore, as there were no differences in behavioural and imaging results between control subjects and the patients for repetition of single words (control condition), which required the same amount of activation of lexico-semantic representations as the STM condition (repetition of word lists), impaired lexico-semantic activation is not likely to account for the results observed in the STM condition. Finally, in a neuropsychological study with the same patients, we explored more directly the relationship between language-processing impairments and verbal STM performance (Majerus et al. 2003b); we showed that all three patients showed no major impairment at the level of lexico-semantic representations, using both standard vocabulary tests as well as more sensitive experimental tasks measuring speed of access to lexico-semantic representations. Furthermore, although two of the patients showed some residual deficits in phonological

processing, the severity of these phonological processing impairments was not related to the severity of the verbal STM impairments for both phonological and lexico-semantic information, thereby showing dissociations between STM storage capacity and the integrity of language representations. Altogether, our results suggest that posterior temporo-parietal areas are specifically related to verbal STM processing and could play the role of a verbal STM buffer, while the results cannot be easily explained by reducing the involvement of these areas during verbal STM tasks simply to the activation of lexico-semantic knowledge. Similar claims have been made by Collette et al. (2001), Giraud and Price (2001), Grasby et al. (1993), and Wise et al. (2001).

To conclude, we argue that the data reported by Ruchkin et al., although consistent with their view of STM as an activated state of language representations stored in posterior brain regions, do not rule out the existence of a verbal STM buffer, which might also be sustained by posterior brain regions very close to those encoding LTM lexico-semantic representations.

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Cognitive neuropsychological evidence for common processes underlying generation and storage of language representations

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Abstract: Ruchkin et al. offer a compelling case for a model of short-term storage without a separate buffer. Here, I discuss some cognitive neuropsychological data that have been offered in support of and against their model. Additionally, I discuss briefly some new directions in cognitive neuropsychological research that bear on the role of attention in Ruchkin et al.'s model.

Speaking and comprehending language take place over time. It is this temporal component of language processing that marks the intersection of memory and language systems. Research efforts have devoted much attention to revealing the organization of each system. The target article by Ruchkin et al. reflects more recent efforts to understand how these two systems are related cognitively and neurophysiologically. The authors provide important evidence supporting a model that attributes temporary storage of language representations to short-term activation of long-term representations without the necessity of a buffer to house the contents of short-term memory (STM).

Cognitive neuropsychological data have been an important source of arguments both for and against the separate buffer model. Evidence supporting an independent buffer comes mainly from case studies of individuals with impaired processing of multiple words in the context of good processing of single words, forming what appears to be a dissociation between word processing and storage systems (Shallice 1988; Vallar & Shallice 1990). The logic of this argument rests on the counter-intuitive assumption that a buffer stores only multiple word sequences. The postulation of a separate buffer is independent of assumptions about the contents of the buffer. Independent buffers are incorporated into models that assume only phonological representations in STM (Baddeley 1986), as well as those that assume short-term stores for all "levels" of linguistic representation (R. Martin & Lesch 1996).

Neuropsychological evidence also supports the model advanced by Ruchkin et al., in which linguistic representations activated during single- or multiple-word processing are maintained

by virtue of the same activation processes that enable activation and retrieval of the representations in the first place. My colleagues and I (Martin et al. 2000) have framed this relationship of language and short-term memory within an interactive activation model of word processing (Dell & O'Seaghdha 1992), with additional components that encode serial order of multiple word sequences (Gupta 1996). In this model, maintenance of activated representations is achieved by two parameters of spreading activation, its strength and its duration. Impairments of single- and multiple-word processing are viewed as disturbances of either or both of these parameters and are assumed to lie on a continuum of severity. Milder activation impairments allow for maintenance and successful processing of single words, but not multiple words, giving the appearance of a selective deficit of verbal short-term memory. More severe activation impairments lead to difficulty in maintaining activation of linguistic representations, even during performance of single-word language tasks, leading to what are typically described as aphasic deficits. In addition to severity of impairment, the ability to maintain activation of linguistic representations in the short term is dependent on the locus of impairment (e.g., semantic, phonological) and task demands.

This model has received empirical support, in part, from studies revealing systematic associations between linguistic and STM impairments (N. Martin & Saffran 1997; R. Martin et al. 1994). Numerous studies indicate that span performance in normal and impaired subjects is sensitive to linguistic variables, including phonological (e.g., Conrad 1964), lexical (e.g., Berndt & Mitchum 1990; Saffran & N. Martin 1990), semantic (e.g., R. Martin et al. 1994; Shulman 1971), and conceptual (e.g., Potter 1993; Saffran & N. Martin 1999) aspects of words. Additionally, in aphasia, span varies based on the nature of the task used to assess span, in conjunction with the nature of the language impairment (N. Martin 1999; N. Martin & Ayala, submitted). Finally, although long-term learning of language is unaffected by impairments affecting storage of phonological representations (e.g., Vallar & Baddeley 1984), it is disrupted in the case of semantic and semantic-STM impairments (N. Martin & Saffran 1990; 1999; Freedman & R. Martin 2001).

Demonstration of these associations is necessary, but not sufficient, evidence for a model that presupposes common processes underlying generation and temporary storage of language representations. Two additional avenues of inquiry provide more definitive support. First, studies of corecovery of word-processing and verbal-STM impairments (N. Martin et al. 1994; 1996) indicate that increased capacity to temporarily store words coincides with improved ability to retrieve words without error. Second, N. Martin & Gupta (2004) demonstrated a severity continuum between impairments of single-word and multiple-word processing, showing that performances on three measures of word processing (auditory lexical decision, picture naming, and word comprehension) correlated with auditory-verbal spans in a group of 50 individuals with aphasia, ranging from mild to severe. These recovery and severity continuum data are consistent with the model advanced by Ruchkin et al. and offer an alternative to the separate buffer model as an account of good single-word processing coupled with impaired multiple-word processing.

Ruchkin et al. propose that prefrontal attentional systems serve to coordinate the short-term activation of posteriorly represented linguistic representations. The role of attentional systems in the breakdown of language and STM functions in aphasia is a relatively recent area of investigation. A study by Hamilton and R. Martin (2002) provides relevant evidence. They demonstrated the presence of inhibition and proactive interference effects in span performance of an individual with aphasia-related semantic impairment, secondary to a lesion affecting the inferior frontal cortex. This is a promising line of research and illustrates, once again, that behavioural studies of impaired cognitive processes, such as language, STM, and attention, can provide important insights into the coordination of multiple systems that bear on performance of verbal tasks.

Historically, many cognitive neuropsychological studies have focused on identifying dissociations among components of cognitive systems, a trend especially evident in the study of verbal STM and language. Recent years have witnessed an increasing focus on the identification of mechanisms underlying cooperation between systems with seemingly different functions. Again, this shift has been especially apparent in the study of relations between verbal STM and language. In this context, it is exciting to consider the converging cognitive neuropsychological, electrophysiological, and imaging data, as reviewed by Ruchkin et al., and their implications for a coherent theory of the coordinated function of attention, short-term (or working) memory, and language processing.

Retention of order and the binding of verbal and spatial information in short-term memory: Constraints for proceduralist accounts

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Abstract: Consistent with Ruchkin and colleagues' proceduralist account, recent research on grouping and verbal-spatial binding in immediate memory shows continuity across short- and long-term retention, and activation of classes of information extending beyond those typically allowed in modular models. However, Ruchkin et al.'s account lacks well-specified mechanisms for the retention of serial order, binding, and the control of activation through attention.

We summarize grouping effects and evidence of verbal-spatial binding in serial short-term memory (STM) that broadly favor proceduralist over modular accounts, but note the limited specification in the target article of mechanisms enabling the retention of serial order, binding, and the control of activation.

Grouping phenomena and mechanisms for retaining items in order. Ruchkin et al. make scant reference to how items are retained in order in STM. Two recently proposed mechanisms for the retention of order are that the constituents of a sequence are associated with (a) temporal context provided by oscillators (e.g., Burgess & Hitch 1999), or (b) serial position markers (e.g., Anderson & Matessa 1997). Patterns of recall errors for grouped lists of verbal items (e.g., 123–456–789) favor the second of these alternatives (Ng & Maybery 2002; 2003). An item recalled out of order typically retains its within-group serial position when it transposes to another group (e.g., item 5 will take the position of item 2 or 8 rather than item 3 or 7), and this pattern of errors is not perturbed when serial position and temporal position are unconfounded (e.g., by doubling the rate of presentation of items in the second group relative to the rate for the other groups). Also, the timing of recall is sensitive to group structure, but not to the precise timing of items at presentation (Maybery et al. 2002). Thus, items do not appear to be coded for order using temporal context provided by oscillators. Rather, order appears to be carried by a hierarchy of position markers that code each item's position in a group, and each group's position in a list. This proposed hierarchy for representing order is compatible with Ruchkin et al.'s proceduralist account, inasmuch as the hierarchy structure is retained within semantic memory (Anderson & Matessa 1997).

Further, grouping of verbal sequences can be induced by discontinuities in pitch, location, or semantic category, as well as time (see Maybery et al. 2002), consistent with the interactive processing of multiple stimulus dimensions, rather than the dedicated processing of phonology. There is also evidence of a longer-term influence of the association of items with serial-position codes, in

that when an item from the preceding trial intrudes on the recall of the current list, it adopts a position in the current list that matches its position in the earlier list (Ng & Maybery 2002). Thus, the purported involvement of a semantic structure in representing order in grouped sequences, the influence of various stimulus dimensions in inducing grouping, and the retention of serial-position coding across trials, are features of this research broadly consistent with a proceduralist account.

Binding of different classes of information in STM. That verbal and spatial information can be represented independently is indicated by experimental (e.g., Farmer et al. 1986), neuropsychological (e.g., Hanley et al. 1991), and neuroimaging (Smith & Jonides 1997) dissociations. However, these studies almost invariably test verbal and spatial STM independently. Maybery et al. (2003) demonstrated that when test conditions force the concurrent encoding of sequences of verbal and spatial information, spatial STM "inherits" susceptibility to irrelevant speech, an effect otherwise isolated to verbal STM. This suggests that concurrent encoding results in binding of the verbal and spatial information. More direct evidence of binding comes from Clissa and Maybery (2003), in which STM for sequences of spatially distributed acoustic stimuli was tested. Recognition judgements were substantially faster when probe stimuli preserved the linkage of acoustic identity and spatial location established in the to-be-remembered sequences than when the probe stimuli consisted of repaired verbal and spatial features. This evidence of identity-location binding was found for nonverbal, as well as verbal, acoustic stimuli, and for retention intervals exceeding the persistence typically presumed for auditory sensory memory. These results suggest continuity between object-based perceptual processes and object-based STM that is consistent with proceduralist accounts, although Ruchkin et al. (2003) do not develop the idea that multimodal "object-focused" perceptual processes might propagate to STM. Their article also does not address precise mechanisms for binding multiple stimulus features. Engel and Singer (2001) suggested that temporal synchrony of neurons processing specific features of stimuli might define those stimuli as integrated events. This possibility should be set against the conclusion from the previous section: Memory for the order of a sequence of events does not appear to rely on the precise temporal coding of those events. It is possible that bottom-up mechanisms relying on temporal contiguity allow the binding of stimulus features into objects, but that the temporal order of these objects is regulated by top-down semantic-based mechanisms detached from any form of temporal signal. However, binding based on temporal synchrony may not provide a complete explanation of the pattern of "inheritance" of interference observed by Maybery et al. (2003). If verbal representations held in one posterior network are corrupted by irrelevant speech, why should this corruption extend to spatial representations held in another posterior network, when all that unites the verbal and spatial representations is their temporal synchrony?

Control of activation through a prefrontal attention mechanism. Perhaps stimulus features could be integrated into more global events or objects through the involvement of pointers maintained in prefrontal cortex, consistent with Ruchkin et al.'s position that a prefrontal attention mechanism based on pointers is used to selectively maintain information in posterior networks. However, what constitutes a pointer and how attention very selectively influences activation in posterior networks remain to be specified. A popular conceptualisation of working memory (WM) is that it provides the workspace for the generation of novel information – either entirely new elements of information or new associations between existing elements. The target article does not explain how there can be selective activation and arbitrary association of informational elements without an excessively elaborate addressing schema for prefrontal pointers, or conversely, how the intrusion into WM of vicarious elements activated through long-term associations is prevented. It will take some care to develop an adequate functional description of pointers while avoiding the charge of duplication levelled against modular models.

Neglecting the posterior parietal cortex: The role of higher-order perceptual memories for working-memory retention

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Abstract: The view that posterior brain systems engaged in lower-order perceptual functions are activated during sustained retention is challenged by fMRI data, which show consistent retention-related activation of higher-order memory representations for a variety of working-memory materials. Sustained retention entails the dynamic link of these higher-order memories with schemata for goal-oriented action housed by the frontal lobes.

The target article by Ruchkin and colleagues provides an integrative model of working-memory retention processes. It is built on the view of working memory as being: activated long-term memory under the dynamic control of an attentional mechanism. This mechanism controls activation in the retention systems and also makes working memory available for goal directed actions. The neuronal substrates of the retention and control mechanisms are identified in posterior cortical areas and in the prefrontal cortex (PFC), respectively. The article reviews electrophysiological and hemodynamic imaging data that substantiate the functional characteristics and neuronal correlates of the model. The high temporal resolution of event-related potentials (ERP) is elegantly and efficiently used to track the time course of the brain systems involved in short-term storage.

We have a lot of sympathy with the model. The identification of brain systems related to working-memory processes, including their timing characteristics; the view that higher-order working-memory systems make use of neuronal networks for lower-order perceptual and motor processes; and the conceptual focus on “memory of systems” as compared to “systems of memory” (cf. Fuster 1995), are particularly strong points.

A limitation of the present model, however, lies in the way hemodynamic imaging data are used to substantiate the functional role of posterior and prefrontal cortical regions during short-term retention. As acknowledged by the authors, a major limitation of hemodynamic imaging techniques is their delayed and prolonged response in comparison with neuronal responses. A second limitation, not adequately addressed by the authors, is the use of block designs and the logic of cognitive subtraction inherent in the PET methodology and the first generation of fMRI studies. The authors take imaging studies of this type (e.g., Courtney et al. 1997) to tentatively support the view that the dorsal and the ventral pathways mediating the sensory analysis of spatial and object information, respectively, also play a key role for short-term storage of both kinds of information. Complementary evidence for the sustained character of the activity in these sensory processing systems is given by confirmatory source analyses conducted on one of their EEG data sets. The imaging studies mentioned above measure sustained activity in retention delays that includes several computational operations, like encoding the stimulus into an iconic store, and transient and sustained storage processes. Given this, the hemodynamic activation of the sensory-specific dorsal and ventral stream in the retention intervals found in these studies could reflect the contribution of material-specific encoding operations, rather than being related to any kind of storage processes, as also suggested by Haxby et al. (1995).

This latter view was supported by an event-related fMRI study of our own (Mecklinger et al. 2000). Similar to the above-mentioned fMRI studies, we used a delayed-response task to examine retention operations for object forms and three-dimensional spatial configurations. By inserting a cue in the retention interval that indicated the type of material to be memorized, we intended to

maximize the contribution of retention processes and to minimize the contribution from encoding processes. In fact, contrasts between brain activation during the retention of both contents and a memory-free control task, exhibited pronounced bilateral activation along the banks of the intraparietal sulcus (IPS) and in prefrontal and premotor areas. Content specificity was revealed in the form of a hemispheric weighting of this IPS-frontal lobes network, with bilateral activation for spatial configurations and left-accentuated activation for object forms. Notably, in contrast to the above-mentioned studies using block designs, no activation in the inferior temporal cortex (i.e., ventral stream) was obtained, even with lowered statistical thresholds. These findings argue against a short-term storage function of the ventral stream for object materials, thus challenging the view of sensory-specific short-term storage functions of the posterior cortex.

The view that the posterior association cortex centered on the banks of the IPS (BA 39 / 40) plays a critical role during sustained retention, is substantiated by a variety of other findings. The IPS is a polymodal representation area that binds sensory-specific features to coherent representations. By this, it entails abstract memory representations that are independent of their sensory origin. Because of their wide distribution in posterior cortex, these higher-order perceptual memories also entail long-term memory components (semantic and episodic) and are more resistant to brain lesions than lower-order perceptual memories, entailing concrete sensations. The role of the IPS as part of a working-memory retention network is further substantiated by its direct and reciprocal connections with the frontal lobes via a substream of the superior longitudinal fasciculus (Petrides & Pandya 2002). Together with its target areas in the posterior and mid-dorsolateral frontal lobe (BA 6 / 8 / 46 / 9), it constitutes a recurrent circuit, forming the neuronal mechanism of working-memory retention. The view that retention is a joint function of posterior parietal and prefrontal regions is supported by an ensemble of hemodynamic imaging studies, showing coactivations of frontal lobe regions and IPS regions during the retention of rather different working-memory materials, including spoken or written words and line drawings of faces and objects (D’Esposito et al. 1998). Furthermore, the EEG coherence study by Sarntheim et al. (1998), which probed the active retention of letter strings and abstract line drawings, revealed the highest anterior–posterior coherence patterns for posterior electrodes that were placed over posterior association areas. To put it differently: Because of our rich experience with the outside world, and our capability to bind perceptual features with facts and events from declarative memory, external events to be maintained in working memory directly activate higher-order perceptual memories, making these memories the most likely memoranda during working-memory retention. Material specificity seems to be expressed in the form of hemispheric weighting of IPS activation, with a weight on semantic/phonological features being expressed as left lateralization and a dominance of episodic features as being bilateral to right activation.

These considerations, although compatible with the “working memory equals activated long-term memory notion,” challenge the view that brain regions which function in the domain of sensory- or modality-specific perception are a constituent part of a neuronal retention network in humans. In our view, it is the polymodal character of the IPS and its capability to house higher-order perceptual memories linked with declarative memories that give these brain regions a key role in the sustained retention of working-memory contents. Whenever retention becomes relevant for action or tasks to be performed, the higher-order perceptual memories are dynamically linked with prefrontal and premotor regions. The hemispheric weighting of posterior activation may also have an influence on which PFC regions get activated during sustained retention. In this vein, the attentional pointer function of the PFC, denoted in the target article, could be reconciled as being the adaptation of perceptual memories to current task demands.

Developmental evidence for working memory as activated long-term memory

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Abstract: There is remarkable agreement between Ruchkin et al.'s psychophysiological views and my own model, based on developmental-experimental evidence, of working memory as activated long-term memory (LTM). I construe subvocal rehearsal as an operative scheme that maintains order information and demands attentional resources. Encoding and retrieving operations also demand attention. Another share of resources is used for keeping activated specific LTM representations.

I find a remarkable congruency between the authors' views, based on psycho-physiological evidence, and my own views, based on developmental-experimental evidence. The latter were expressed in a formal model of verbal short-term memory tasks (Morra 2000). I summarize here some assumptions of that model, and highlight their parallels with the target article.

First, words are represented in LTM as cognitive units (figurative schemes). When stimulus items are presented, encoding operations enable activation of those units. The encoding is automatic in the case of auditory presentation, but effortful for visual items. This is congruent with the general thesis of activation of LTM representations, defended in the target article, and with its particular statements on processing streams and phonological recoding (sect. 3.1). In turn, the idea of activated LTM representations is also congruent with other similar models of working memory (e.g., Cowan 1988; 1999; Engle et al. 1992; Pascual-Leone 1987; Shiffrin 1976).

Second, subvocal rehearsal is an optional strategy, which yields the benefit of encoding order information in a simple way. In itself, the rehearsal procedure is a LTM representation (an operative scheme for repeating speech materials); its activation also demands a share of the individual's limited attentional resources. Most often, rehearsal is useful because its benefit is greater than its attentional cost. However, young children may not rehearse (although they are obviously able to repeat speech), because this strategy demands too large a fraction of their very limited attentional resources. An alternative strategy could be just to try to keep activated the single relevant LTM units, without specific encoding of order information. These assumptions on rehearsal seem consistent with the authors' claims on "rehearsal operations" that involve attentional control and storage (i.e., LTM representation) of attentional control operations in the frontal cortex (sects. 3.1 and 5).

Third, yet another operative scheme is involved in retrieval and, in order to be activated, it also consumes attentional resources. This assumption does not have a direct parallel in the target article, which does not address overt recall, but is broadly consistent with its claims on control operations.

Fourth, because the operative schemes currently used for encoding, rehearsal, or retrieval consume attentional resources, it follows that only a part of the individual's limited attentional capacity remains available for activating LTM representations of the stimulus words. This is consistent with (and perhaps more specific than) the authors' suggestion that the amount of information in the focus of attention is limited (sect. 5).

Fifth, phonological encoding often prevails for various reasons, such as automatic recoding of an auditory input, or usefulness of phonological rehearsal. However, phonological encoding is not the only possibility. The cognitive units used by a participant to represent stimulus items could also be semantic codes, number codes in the case of digit-span tasks, or any appropriate representation of lexical items. The nature of the particular codes that participants use may affect the rate of decay or the amount of interference among those representations that do not remain fully activated, because they cannot be kept within the focus of atten-

tion. This seems consistent with sections 3.2 through 3.4 of the target article.

A model with only one free parameter was tested successfully for goodness of fit in a series of experiments with primary-school children, also reported by Morra (2000). Therefore, we have behavioral data from experimental developmental research that supports a model based on the general view of working memory as activated LTM.

What about the alternative view, that working memory is accounted for by specific buffer stores, perhaps coordinated or supervised by an executive control system? If one assumes that there are specific short-term stores, then one should also specify their limitations. This task proved awfully difficult; for example, some valuable reviews (Cornoldi 1995; Logie 1995) noted that it is problematic to define the capacity limitation, or even the appropriate measurement unit, for visual and spatial short-term storage. However, one important exception is that the limited capacity of the articulatory (or phonological) loop seemed to be well-established, that is, people, both adults and children, can remember as much as they can rapidly utter in 1.5 or 2 seconds (e.g., Baddeley 1986). Such an estimate was based on the word-length effect, and particularly, the ratio of recall to articulation rate, or the slope of the regression equation of recall on articulation rate (given a near-zero intercept in the equation). This seemed to be the only precise statement on capacity limitations generally agreed upon by supporters of the "buffer stores" view of working memory.

Our results were in contrast with this claim; more important, different and inconsistent estimates of the capacity of the hypothesized articulatory loop were obtained across experiments, conditions, and techniques of estimation (Morra 2000). In our experiments, the finding of a word-length was replicated, as well as a correlation between rate of articulation and recall, which suggests that rehearsal skill actually contributes to memory performance. However, it seems that an appropriate account of the role of rehearsal has to be different from that proposed within storage frameworks.

Moreover, previous experiments from our laboratory (e.g., Morra 1989; 1990; Morra et al. 1993) suggested the conclusion that the quantitative predictions of the articulatory loop model were also not supported in experiments with adult participants. It seemed to us that the classical findings of a near-zero intercept in the regression equation and a constant capacity of the articulatory loop (measured in units of time) were due, at least in part, to the particular features of the experiments from which those results were found, such as the use of supra-span memory lists and the English language. Publishing those results proved extremely difficult (see Morra 1998; 2001; see also Anderson & Matessa 1997); however, from other studies too (e.g., Cheung & Kemper 1993; Hulme et al. 1991; Nicolson & Fawcett 1991) we now know that language and span versus supra-span procedure do actually affect the relationship of short-term recall to rate of articulation.

Thus, studies with adult participants have already suggested that the time-limited capacity of a short-term phonological storage system is questionable. Our experiments with children (Morra 2000) only strengthened this conclusion. The target article also reaches the conclusion that the existence of separate buffer stores for short-term memory is questionable. It is interesting to note, at this point, how well our conclusions agree, even though they are based on such different lines of research.

Another minor comment on developmental matters concerns the statement in the target article that phonological rehearsal plays a critical role in language acquisition. This may be true; however, it is worth noting that an alternative interpretation has been suggested (e.g., Bowey 2001), according to which, children's non-word repetition essentially depends on the clarity and distinctiveness of phonological representations in long-term memory. Such an account seems particularly consistent with a view of working memory based on currently activated long-term memory.

How does the attentional pointer work in prefrontal cortex?

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Abstract: The current model, based on event-related potential (ERP) studies, posits that the working-memory system is a state of activated long-term memory; this appears comprehensive, but it needs further detailed analysis of functional neural connectivity analysis within the prefrontal cortex (PFC) and between the posterior and prefrontal cortex. Specifically, the role of dorsolateral PFC and anterior cingulate cortex (ACC) is probably critical for PFC's attentional controller. Neural implementation of the executive function in working memory appears critical to build a firm model.

The issues regarding how short-term storage is neurally implemented, and how it is related to long-term memory, are critical for modeling working memory (Baddeley 1986). By introducing the working-memory system as a state of activated long-term memory, Ruchkin et al. have reviewed models that explain how "short-term storage mechanisms involve an increase in neural synchrony between prefrontal cortex and posterior cortex and the enhanced activation of long-term memory representations of material held in short-term memory" (target article, Abstract). Ruchkin et al. insist there is no need to posit specialized neural systems whose functions are limited to those of short-term storage buffers in connection with the role of prefrontal cortex's (PFC) attentional pointer for maintaining activation in the posterior processing systems. My first argument is based on the modality- and material-specific buffers in the posterior cortex, and the second one is based on neural correlates of PFC's attentional controller.

I agree with the views (e.g., Cowan 2001; Crowder 1993) that short-term memory stores are constituted by an activated subset of long-term memory. However, an activated subset appears to somehow involve modality- and material-specific properties. In two functional magnetic resonance imaging (fMRI) studies, using the reading and listening span tests (RST and LST) which measure verbal working-memory capacity by reading (listening), we (M. Osaka et al. 2003; N. Osaka et al. 2003b) asked the subject under fMRI investigation to retain the specified word, while judging as true or false the semantics currently in process (dual task). We found the activated brain areas in the posterior (BA18/19) and superior temporal/inferior parietal (BA22/42) during the RST and LST tasks, respectively. However, interestingly enough, we also found commonly activated loci, which are located in the PFC's dorsolateral prefrontal (DLPFC), inferior frontal gyrus (IFG), and anterior cingulate cortex (ACC) (M. Osaka et al. 2003; N. Osaka et al. 2003b). These data suggest modality- and material-specific areas in the posterior brain are still at work, in coordination with PFC, even if these are a portion of an activated subset of long-term memory. Because of the low temporal resolution of the system, our fMRI data could not provide the comparable data for material that is heard or read, as mentioned (Penney 1989; Ruchkin et al. 1990).

The second argument is based on the neural basis of PFC's attention pointer system. Ruchkin et al. refer to PFC's attentional pointer system for maintaining activation in the appropriate posterior processing system, and the number of pointers involved in the PFC determines the attentional constraint of the working memory. In my view, attentional pointers are likely the resource-limited agent of the executive functions, which work in a coordinated fashion to achieve task-defined goals (cf. M. Osaka et al. 2002). The authors of the target article did not show, in detail, how the pointer system works under specified neural implementations in PFC. Our fMRI data show that DLPFC, IFG, and ACC are the distributed executive areas in PFC which work together to control posterior brain functioning in a task-dependent manner. We also showed a critical role for individual differences in PFC functions:

Individuals having higher working-memory capacity show higher functional connectivity between ACC and DLPFC (M. Osaka et al. 2003), whereas individuals having lower working-memory capacity show lower connectivity among ACC, DLPFC, and modality-specific posterior regions.

Thus, our fMRI investigation is likely to support the idea that the posterior cortex provides the representational basis for most short-term memory operations, and the PFC provides the attentional control, as the target article authors argue. The other example, suggesting PFC's top-down control that extends activation into the posterior cortex, was shown in an fMRI experiment in which an onomatopoeic word, suggesting visual images of strong laughter heard by the ear, evoked top-down visual awareness of the laughing face in the brain (N. Osaka et al. 2003a). The laughter word clearly activated the lingual gyrus/fusiform gyrus area, commonly known as the "face area." Further neuronal network-based connectivity studies are needed to establish a model describing working-memory systems as a state of activated long-term memory.

Will the unitary view survive the short- and long-term?

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Abstract: In this commentary, we focus on four points. First, we discuss the assertion that the unitary model explains dissociations that implicate multiple systems. Second, the distinct nature of information utilized in immediate- and delayed-recall supports the distinct memory systems view. Third, the variable nature of capacity limits corroborates this view. Finally, we review event-related fMRI results that suggest support for multiple systems.

Ruchkin and his colleagues argue that, in contrast to the multiple-component view of memory proposed by Baddeley and Hitch (1974), a unitary-system view provides a better and more parsimonious account of data in the extant literature. In this view, working-memory (WM) retention involves the activation of long-term-memory (LTM) representations, mediated by binding circuitry in prefrontal cortex (PFC). We will comment on several claims made by Ruchkin et al. The first is a plausibility claim: Specifically, that key empirical findings (e.g., neuropsychological data showing STM/LTM dissociations) are readily interpretable within a unitary-system framework. The second claim is that data from event-related potentials (ERPs), with superior temporal resolution, provide evidence that permits critical tests of the unitary- and multiple-component views. The third claim is that fMRI evidence complements the ERP data to further support a unitary-system account of WM.

The plausibility claims made by Ruchkin et al. underscore the fact that experimental results may be variably interpreted to support more than one theoretical system. The authors point out, for instance, that the double dissociation, wherein some patients demonstrate STM deficits (e.g., Shallice & Warrington's 1970 patient, KF) in the presence of preserved LTM, whereas others demonstrate LTM deficits in the presence of preserved STM (Scoville & Milner 1957), may be accounted for by a deficit in binding processes that activate LTM representations. There are two lines of evidence that render this account problematic. First, it is troubling for the binding-deficit explanation that patients with these deficits have lesions in focal, but distinct, brain regions. Additionally, these patients' lesion sites do not match the regions implicated in an fMRI study of binding (Prabhakaran et al. 2000). Second, Baddeley and Wilson (2002) have observed that amnesics apparently are able to integrate information in LTM to remember

ideas from connected prose. The problem for these patients appears to be in their ability to consolidate new information into LTM. Thus, they form temporary representations that use LTM, but these representations cannot be stored in LTM. Considerations such as these suggest that the unitary-system view does not necessarily provide a more plausible account of available literature than does the multiple-component view.

A truly plausible account of the available literature must be able to explain fundamental and well-established laboratory phenomena. For example, the word-length effect, wherein fewer long words can be retained over a delay interval than short words, suggests that these STM representations are minimally distinguished on the basis of their meaning and are principally phonologically-based (Baddeley et al. 1975). If, as the unitary account claims, information in the focus of attention is activated from long-term memory, one would expect the activated representations to be maximally distinguishable based on the rich and semantically elaborate nature of long-term representations. Similarly, the semantic nature of LTM representations would seem to inoculate them to the confusability created by phonologically similar items in to-be-retained lists. Yet, such confusability is reliably observed in the laboratory (Baddeley 1966a; 1966b; Baddeley & Dale 1966). A possible clue to explain the emergence of these effects is the observation of phonological similarity and word-length effects in sign language (Ronnberg et al. 2000; Wilson 2001). This differs from the typical description of the sketchpad in nonsigners, which indicates that sequential information is not well-maintained by the visuospatial sketchpad (Baddeley 2001a).

An explanation of capacity limits has been considered central to completely understanding the architecture of the human mind. The unitary system provides one plausible account, based on limitations of the focus of attention. However, the unitary-system account cannot easily explain observed capacity-limit differences that depend on the composition of to-be-remembered lists. That is, immediate memory for a list of randomly ordered words averages between 5–7 words, but memory for words in sentences averages between 13–22 words (Craik & Masani 1969). Additionally, it has been demonstrated that capacity limits can be overcome by training individuals to chunk information (Ericsson et al. 1980). The observation of multiple capacity limits implies the operation of multiple memory systems. Chunking in retrieval structures apparently can be used to overcome capacity limits, but their role in a unitary memory system is not clear (Ericsson & Kintsch 1995; Gobet et al. 2001).

Ruchkin et al. argue that the superior temporal resolution offered by ERP can yield evidence to distinguish between unitary- and multiple-systems views. Although it is indeed true that ERP does offer superior temporal resolution, many of the changes in the data they show occur on the order of four seconds or more, a time scale certainly resolvable by fMRI (Zarahn et al. 1997). Moreover, more precise evidence for the claims made by Ruchkin et al. may come from techniques with superior spatial resolution, such as fMRI. Under these circumstances then, ERP and fMRI should converge, and, in fact, they do. In a number of studies, for example, PFC activation similar to that shown by Ruchkin et al. has been observed (Rypma & D'Esposito 1999; 2000; 2001; Rypma et al. 1999). These studies complement the results shown by Ruchkin et al. to the extent that they show activation increases in PFC following onset of to-be-remembered information. Further, they show distinct activation topographies based on whether to-be-remembered lists were short (i.e., 2–3 letters) or long (i.e., 6 letters). That is, ventral regions of PFC showed activation during retention of both short and long lists. Dorsal PFC, however, showed a more load-sensitive activation pattern. That is, there was minimal activation during retention of the short list, but substantially increased activation during retention of the long list.

In summary, although these results do not provide a critical test between the multiple and unitary working-memory theories, they do support the notion that multiple cortical regions are involved

in STM maintenance, depending on task demands. We interpret these results to indicate the existence of separate STM systems used to support information retention under high-memory-demand conditions.

The short-term dynamics within a network of connections is creative

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Abstract: Although visual long-term memory (VLTM) and visual short-term memory (VSTM) can be distinguished from each other (and from visual sensory storage [SS]), they are embodied within the same modality-specific brain regions, but in very different ways: VLTM as patterns of connectivity and VSTM as patterns of activity. Perception and VSTM do not “activate” VLTM. They use VLTM to create novel patterns of activity relevant to novel circumstances.

There is strong evidence for several components of Ruchkin et al.'s thesis, including much that is stronger than that which they cite. I was surprised to see a review of the role of prefrontal cortex (PFC) in working memory (WM) that neglects the work of Pat Goldman-Rakic. Furthermore, although Ruchkin et al. distinguish between different components of visual memory, they make no use of the first and strongest evidence distinguishing SS, VSTM, and VLTM (Phillips 1974; 1983b; Phillips & Christie 1977a), nor do they relate them to general purpose processing capabilities, such as those thought to involve PFC (Phillips & Christie 1977b). The possibility that temporary dynamic storage involves activity within a network in which LTM is embodied in the connection strengths is an idea of great antiquity, for which there is ample evidence. Phillips (1983b, Fig. 1) presents just one of many versions of this idea as applied to visual memory. This does not imply that VSTM occurs within *the same* systems as those that are initially processing the information, however. The regions within which SS occurs are included in the latter, but not the former (i.e., that in which VSTM occurs). If activity in striate and peristriate areas could be maintained, then SS (photographic or iconic memory) would be a voluntary option. It is not (Phillips 1974; 1983b; Phillips & Singer 1974; Simons & Levin 1997). Thus, WM is possible within some cortical regions, but not others. The evidence reviewed by Ruchkin et al. suggests that voluntary maintenance may not be possible in regions of the visual stream prior to its division into dorsal and ventral pathways.

The dependence of short-term dynamics on long-term changes in connectivity are so important for our understanding of cognition that it is necessary to ask whether the notion of “activation” clarifies this relationship. I don't think that it does. First, activity and connectivity are very different things. Neural network studies clearly show that the short-term dynamics of a network with recurrent connections can be very complex, and evolve on a short-term time scale into many different patterns of activity, without any changes in the connection strengths. Second, Ruchkin et al. use the word “activation” in several different ways, and their equivalence is far from obvious. Sometimes they use it in a psychological sense, sometimes to refer to EEG measures, and sometimes to refer to underlying neuronal activity. The relation between the latter two is distant, and that between both of these and the former is even more distant. For example, the ordinate in their Figure 3 refers to “activation,” but it doesn't seem to really mean measured EEG activity, as in some of their other figures. It is even harder to relate Figure 3 to neuronal activity, as the activity of neurons in the visual cortex has a far more complex time-course in response to stimulation than that given in Figure 3 as a representa-

tion of iconic activity. For example, contrast Ruchkin et al.'s Figure 3 with Figure 1 in Phillips (1983a), which is based upon the single-unit neuronal activity reported in Singer and Phillips (1974). Third, "activation" connotes the selection of old things, not the creation of new things. Even pre-attentive perceptual processes must involve the latter (Watt & Phillips 2000).

There is space here to outline only two paradigms in support of my view that the creation of new descriptions cannot usefully be viewed as simply the activation of old items. The first involves the use of matrix block patterns to compare VSTM and VLTM (Phillips 1983b; Phillips & Christie 1977a). To focus on visual memory, these patterns were designed to be difficult to verbalize adequately. To focus on the use of novel descriptions, rather than on the use of old items, novel patterns were used on every trial. The results clearly showed that accurate descriptions of novel patterns could be voluntarily maintained for as long as the subject could keep attending fully to them, providing the matrix patterns were below measured levels of complexity. Some VLTM for those patterns was produced by a single presentation, but with much less accuracy than for VSTM. I cannot see how it is useful to think of these VSTM descriptions as activation of long-term memory items, unless by "activation," Ruchkin et al. mean the use of descriptive capabilities stored in VLTM to create novel descriptions.

The second paradigm involves mental rotation. To see whether rotated images formed within VSTM operate upon the long-term representations of the items rotated, we modified a paradigm that studies discrimination between normal and mirrored versions of familiar alphanumeric characters displayed in various orientations (Shepard 1978). Our results show that when subjects image a familiar alphanumeric character upside down they still have the upright character in VLTM available for use (Roldan & Phillips 1980). This shows that mental rotation uses knowledge of the form of the upright character and transformational rules to create a novel description within VSTM. They do not transform the VLTM of the familiar form.

I assume that there will be general agreement with Ruchkin et al.'s view that many modality-specific brain regions embody both VSTM and VLTM. I do not see how the concept of "activation" advances our understanding of these issues, however. That said, my reservations concerning the conceptual framework within which Ruchkin et al. interpret their data do not imply that measures of the kind they emphasize are without value. Many, such as those of EEG coherence, may well be of value, if validly related to the underlying neuronal activity.

Models versus descriptions: Real differences and language differences

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Abstract: We argue that an approach that treats short-term memory as activated long-term memory is not inherently in conflict with information recycling in a limited-capacity or working-memory store, or with long-term storage based on the processing in such a store. Language differences aside, real model differences can only be assessed when the contrasting models are formulated precisely.

The authors of the present target article introduce their proposal in an attempt to draw a distinction between the idea of short-term or working memory as a separate store and the idea of short-term or working memory as activated representations in long-term memory. We note that these views are not inherently opposed to one another. In particular, it makes a great deal of sense to assume

that short-term memory corresponds to activated representations in long-term memory, but that does not mean that a model for short-term memory that is based on the notion of stores or buffers is useless or even incorrect.

In this respect, it is of some interest to note that the Short-Term Store (STS) system in the modal model of memory proposed by Atkinson and Shiffrin (1968) has long been formulated as the temporarily activated portion of Long-Term Store (LTS) (e.g., Atkinson & Shiffrin 1971). This reformulation was based on theoretical grounds: in particular, the idea that it made more sense to assume that perceptual stimuli contact information in long-term memory, rather than to assume a sequence from sensory registers to short-term store to long-term store. This idea was further elaborated in Shiffrin (1975; 1976). Of course, the idea of short-term memory as activated representations in long-term memory considerably predates Atkinson and Shiffrin, going back, at least, to James (e.g., 1890).

More importantly, this idea is easily reconciled with a model that assumes that STS or working memory may be viewed as a store that temporarily holds a small amount of information for further (more elaborate) processing. As argued by Shiffrin (1975; 1976), perceptual information activates a large amount of long-term memory information. However, the information is rapidly lost from STS (i.e., becomes inactive) unless it is maintained in STS through rehearsal and other coding processes. As a result, only a few items may be maintained simultaneously in a highly active state in STS. A STS buffer, such as that proposed by Atkinson and Shiffrin (1968), is a simple model used to describe this process of maintenance of information in STS.

The history of the psychology of memory has shown a number of examples where ideas that are not necessarily mutually exclusive lead to unfruitful debates. Perhaps the clearest example is the way in which the Atkinson–Shiffrin modal model of memory is usually discussed in textbooks and put into opposition with the levels-of-processing framework (Craik & Lockhart 1972) or the working-memory model of Baddeley and Hitch (1974; 1977). The target article echoes these textbook accounts when it mentions that "the modal model . . . does not provide an accurate account of how short-term and long-term memories interact, nor does it correctly predict performance for certain dual-task experiments" (sect. 1.1). However, Raaijmakers (1993) and others (Bjork 1975; Glanzer 1977; Shiffrin 1977) have argued that the conflict between the levels-of-processing approach and the Atkinson–Shiffrin model is artificial and not based on a detailed analysis of the Atkinson–Shiffrin model. In particular, it does not take into account the role assigned to the control processes of rehearsal and coding (or maintenance and elaborative rehearsal). In a similar vein, it has been argued that the evidence that was put forward by Baddeley and Hitch (1974) does not really contradict the modal model (see Raaijmakers 1993).

We are afraid that the present target article might similarly promulgate a false dichotomy and help initiate a flood of papers showing either the fruitfulness of the "store"-approach or arguing for the temporary-activation approach. Although some might see such a state of affairs as a sign of healthy progress, active debate is not always a good thing when the debaters are talking "past one another." We believe that such theoretical controversies are best resolved by careful and precise formulation of the different approaches, so that the fundamental and underlying similarities and differences can be assessed. Our personal approach has been to produce such specification by formulating mathematical and computer-simulation models. We predict that such formulations would show that the two model types are not in conflict, but rather that each type has many differing variants that would be amenable to experimental testing. In addition, the choice of model representation may be more a matter of style than substance. The preferred choice of "stores" or "activated subset" will probably depend most on the nature of the data that one tries to accommodate, and an assessment of which approach proves more fruitful, parsimonious, or productive. As such, the situation is reminiscent of the wave versus particle viewpoints in contemporary physics.

Working memory as a state of activated long-term memory: A plausible theory, but other data provide more compelling evidence

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Abstract: The identity of working-memory and long-term memory representations follows from many lines of evidence. However, the data provided by Ruchkin et al. are hardly compelling, as they make unproved assumptions about hypothetical generators. We cite studies from our lab in which congruent slow-wave topographies were found for short-term and long-term memory tasks, strongly suggesting that both activate identical cell assemblies.

The idea that short-term memory is the currently active information in long-term-memory has a longer tradition in experimental psychology than indicated in the target article. Shiffrin and Schneider (1977) already made this claim, and they also introduced an “attention director” as a device that keeps STM representations active. Atkinson and Juola (1974) borrowed concepts from the theory of signal-detection to model response times in memory-search paradigms, irrespective of whether the representations had the status of transient or permanent representations. More recent approaches that model learning, storage, and retrieval by means of artificial neural networks come to very similar conclusions, namely, that knowledge is stored in exactly those cortical areas in which on-line processing during a first encounter of percepts takes place (McClelland et al. 1995). Finally, evidence from neuropsychology supports the idea that lesions of posterior “perceptual” cortical areas result in a loss of memory representations (Damasio 1989), and that the prefrontal cortex exerts “control” over posterior areas to maintain working-memory traces (Chafee & Goldman-Rakic 1998; Petrides 2000).

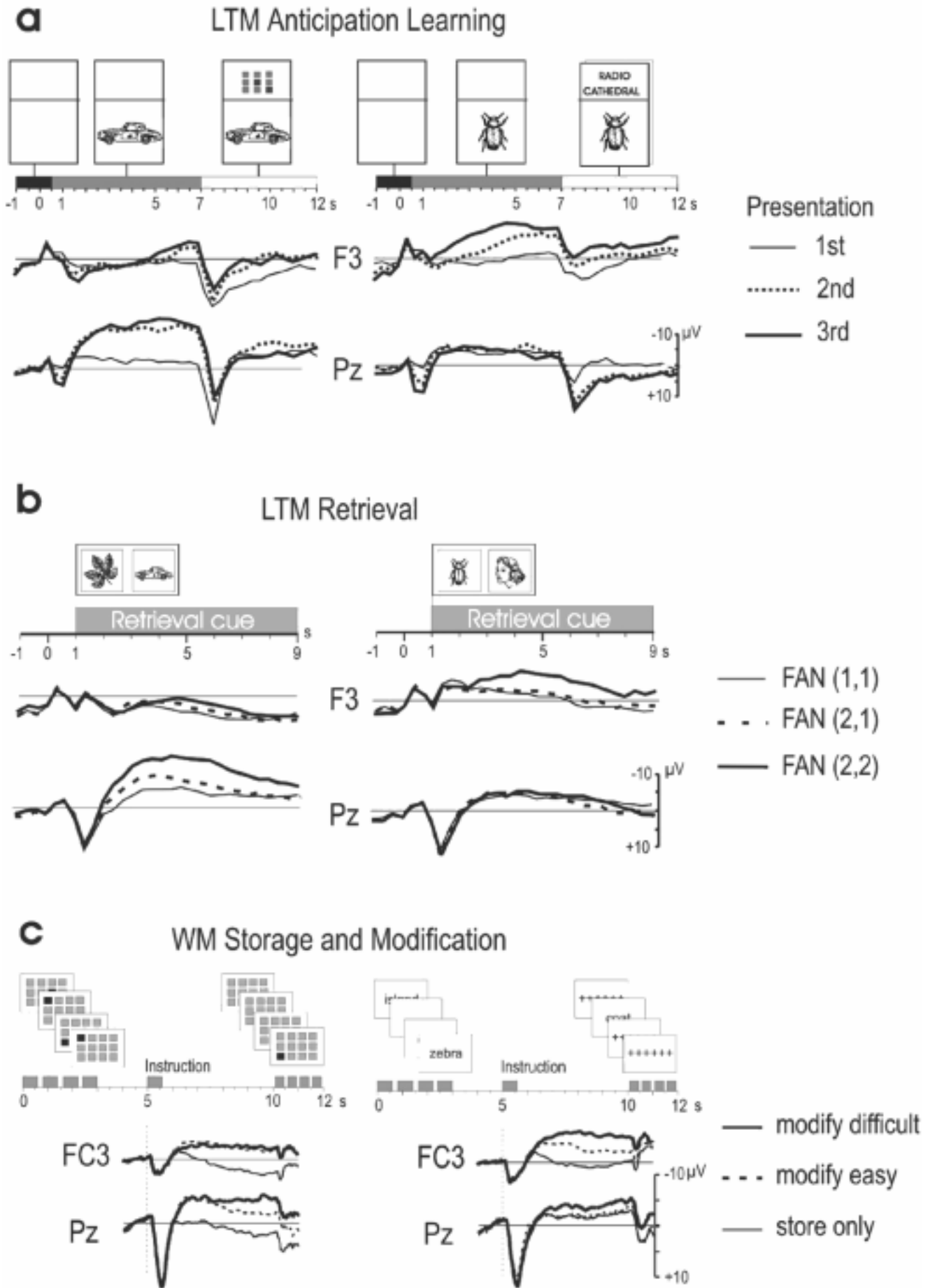
In light of this evidence, it has to be asked whether the data presented by Ruchkin et al. do provide new and compelling evidence in support of the general framework. No doubt, the data are new, and they show distinct topographies for different working-memory tasks, but the relationships, as they are drawn by Ruchkin et al., between event-related potentials (ERPs) and their neuroanatomical bases and between activation patterns and processing models, are rather vague. Their main argument, that working-memory contents are held in posterior areas and attentional control over these areas is exerted from prefrontal areas, is based on the location and timing of generator functions estimated from the ERPs by means of Scherg’s Brain Electrical Source Analysis (BESA) model. However, it is well known that the exact location of generating dipoles cannot be estimated unequivocally from sur-

face potentials. The “inverse problem” has no unitary solution (Nunez 1981) and a different model from the one implemented in Scherg’s algorithm can produce a completely different picture. For example, using a minimum-norm model and changing one parameter only, the same set of data can either be explained by a few narrowly circumscribed dipoles or by a broadly distributed set of many dipoles (Haan et al. 2000). So, generator functions can hardly be crucial for the localization and timing of functionally specialized cell assemblies. Hence, the time courses of the hypothetical processes (shown in Figs. 3 and 7 of the target article) are plausible, but not backed at all by the ERP data cited.

The only strong evidence provided by Ruchkin et al.’s data is that distinct generators must be involved in the various working-memory tasks. However, does this finding support the idea that working-memory contents are just the activated representations of long-term memory information? This is questionable. The observed distinct topographies could also be taken to be in support of a model that postulates working-memory stores separate from long-term memory stores.

Within the methodological limits of ERP research, a closer link between working memory and long-term memory is nevertheless possible. A prediction derived from the framework is that topographies for working-memory and long-term memory tasks should be congruent, provided the activated representations are the same. Such a topographic congruency could be proved in a series of studies in which long-lasting negative slow waves were recorded (Rösler et al. 1997). Among others, we could show that storage and retrieval of long-term memory contents produced a distinct topography, depending on whether the information was spatial or verbal (Fig. 1a and 1b). This topography was, by and large, the same as when spatial- or verbal-memory contents had to be manipulated in working memory (Fig. 1c). Moreover, in both cases, the slow-wave patterns were not only distinct for the different materials, but the maximum amplitude of each slow-wave pattern varied systematically with the task demands, as well. More demanding long-term memory search and more demanding working-memory transformations resulted in an increase of a negative slow wave with a maximum at left-frontal areas for verbal material and at parietal areas for spatial material. Thus, these studies not only prove a distinct topography for different representations, but also that each topography is specifically modulated by the task demands. Moreover, the congruent topography strongly supports the idea that working memory and long-term memory contents are activated within the same cortical areas (Rösler & Heil 2003).

Figure 1 (Rösler & Heil). (a) Participants (Ppts) learned associations between line drawings and grid positions (left) or words (right). First, a line drawing was presented and seven seconds later, one or two associated positions or words appeared. With the first presentation, all curves are flat except for the stimulus evoked potentials. However, as soon as the associations can be anticipated (second, third presentation), a slow wave emerges with a material specific topography – the maximum is over the left frontal cortex with verbal, and over the parietal cortex, with spatial information. (b) LTM-retrieval of the material learned one day earlier. Ppts saw two line drawings and they had to decide whether the two were associated via a common position (left) or via a common word (right). Each drawing could be associated with one or two mediators (grid positions or words) and this resulted in the three levels of fan. The slow wave increased with increasing fan, that is, increasing retrieval difficulty, and this enlargement had the same task specific topography as the amplitude increase during learning (data from Heil et al. 1997). (c) Storage and modification of working memory contents. Ppts saw a sequence of grid positions (spatial information, left) or of words (verbal information, right). On command of an instruction stimulus, the sequential order of the series had to be kept (storage) or changed in a simple or a more difficult manner (modify easy vs. difficult). Finally, Ppts had to match the contents of WM against a new sequence of frames. A substantial slowwave appeared while the subjects modified the sequential order of the stimuli. The maximum effect was located over the parietal cortex with spatial material and over the left frontal cortex with verbal material (data from Rolke et al. 2000).



The contribution of long-term memory and the role of frontal-lobe systems in on-line processing

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Abstract: Ruchkin et al. ascribe a pivotal role to long-term memory representations and binding within working memory. Here we focus on the interaction of working memory and long-term memory in supporting on-line representations of experience available to guide on-going processing, and we distinguish the role of frontal-lobe systems from what the hippocampus contributes to relational long-term memory binding.

Ruchkin et al.'s current treatment emphasizes a view of working memory as the activated portion of long-term memory, with frontal-lobe working memory systems serving as attentional "pointers" to long-term memory representations held in posterior cortex processors, and also serving to integrate or bind such materials in memory.

In this commentary, we commend their formulation for focusing on the active role of working memory, rather than on a more passive short-term memory storage capacity, but argue that: (1) the on-line representations that guide on-going performance are more than just the contents of working memory; (2) frontal-lobe systems play an even more active role in on-line processing, beyond merely maintaining representations, than that articulated by Ruchkin et al.; and (3) the binding functions accomplished by the perceptual and/or attentional systems in service of on-line processing and held in working memory are *not* the same as the relational memory binding accomplished by the hippocampus in forming new *long-term* relational (declarative) memories. These points are discussed in turn.

First, regarding the aspects of memory available to guide on-line processing, many studies point to the pivotal role of long-term memory representations. For example, Loftus and Mackworth (1978) demonstrated that people fixated earlier and more often those items within a scene that were semantically inconsistent, such as an octopus in a farm scene, compared to items that were semantically consistent with the scene's context. Reingold et al. (2001) demonstrated a perceptual encoding and working-memory advantage for chess experts over novices in a change blindness flicker paradigm (see also, Chase & Simon 1973). These studies, together with the work presented by Ruchkin et al. (2003), indicate the availability of long-term memory representations to guide subjects' viewing and performance. But, in addition to having working memory, comprised of active, recently processed information available to conscious awareness, there is also available information from activated long-term memory representations *outside of conscious awareness*, which combine to constitute what we have termed the on-line representation (Ryan 2001; Ryan & Cohen 2001; under revision). Thus, we have shown in change-detection paradigms that on-line processing, as measured by how viewers actively move their eyes around visual scenes, is guided by both consciously aware and consciously unaware aspects of representations of their recent previous experience, entailing the integration and comparison of recently processed information regarding the external world with active representations, only some of which are consciously accessible.

Second, evidence from neuroimaging studies indicates clearly that the frontal cortex is more than just a pointer of attention to long-term memory representations supporting maintenance of information. For example, Petrides, Owen, and colleagues have shown that, whereas the ventrolateral prefrontal cortex is activated when information must be maintained and monitored, the dorsolateral prefrontal cortex is active when the recently processed items must be *manipulated* to guide the appropriate be-

havioral response (e.g., Owen et al. 1996; Petrides 1995). Much subsequent work has also focused on frontal-lobe activity associated with manipulation of representations, thereby emphasizing the working-with-memory element of working memory. Wagner et al. (2001) have extended these findings. In addition to the dorsolateral prefrontal cortex being preferentially active during maintenance and selection, but not monitoring of, phonological information, activation within the dorsolateral prefrontal cortex lagged behind that of the ventrolateral prefrontal region. The authors interpret their findings as suggesting that representations were already active and being monitored via the ventrolateral cortex and were then available for manipulation by the dorsolateral prefrontal cortex.

Third, we turn to the issue of binding of elements of activated information, and the relation between frontal-lobe working-memory systems and hippocampal-mediated long-term memory. In our recent eye-movement work (Ryan & Cohen, in press), we demonstrated that amnesic patients can maintain enough information regarding scenes, and the relations among the elements within scenes, during a short delay, so that their eye movements are attracted to regions of relational change within the scenes (e.g., being attracted to now-empty regions that were formerly occupied). These eye movement effects were fully comparable to those observed in normal control subjects. However, when longer delays were imposed between the initial and subsequent viewing of the scenes, amnesic patients selectively failed to show these effects of memory for relations. Thus, information about the constituent elements of scenes could be bound together and held in working memory to guide on-line performance, on the basis of systems outside of the hippocampus, presumably involving frontal cortex. But binding of such relational information into long-term memory representations critically requires the hippocampus.

Related findings were reported by Waltz et al. (1999), who reported that patients with temporal-lobe degeneration showed impaired performance on recognition memory, yet spared performance for relational processing in the transitive inference task, whereas patients with prefrontal damage showed the reverse pattern of performance. These findings from amnesic patients and patients with frontal-lobe impairment suggest that the processes engaged within short-delay tasks, even in support of relational processing, are not the same binding processes supported by hippocampal-system structures in forming long-term relational (declarative) memory representations.

We suggest that the posterior cortices parse incoming information into distinct items, which are then monitored and kept active along with long-term memory representations by the prefrontal cortex, as suggested by Ruchkin et al. The prefrontal cortex then is able to manipulate these items in a flexible manner that promotes the *processing* of relations over a short delay. In contrast, the hippocampal system supports the *binding* of the relations among distinct items in long-term (declarative) memory. Thus, the prefrontal cortex itself does not perform relational memory binding, nor do binding processes form the basis of working memory. Rather, the frontal cortex serves to manipulate and compare recently processed item information with any existing representations, so that further action, including behavioral responses, may be guided appropriately. In this regard, the frontal system permits items to be manipulated and organized, but no enduring links are established between items in long-term memory unless the participation of the hippocampus is recruited.

The short-term/long-term memory distinction: Back to the past?

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Abstract: The view that short-term memory should be conceived of as being a process based on the activation of long-term memory is inconsistent with neuropsychological evidence. Data from brain-damaged patients, showing specific patterns of impairment, are compatible with a vision of memory as a multiple-component system, whose different aspects, in neurologically unimpaired subjects, show a high degree of interaction.

In the late 1960s, neuropsychological evidence showing that brain damage may bring about selective patterns of memory impairment, closely mapping onto current functional constructs of putatively independent components, such as short-term and long-term memory, provided the main and definitive evidence supporting the distinction between short- and long-term retention systems. This two-stage distinction paved the way to the further fractionation of memory, which took place in the following two decades (Baddeley et al. 2002). The arguments developed by Ruchkin et al., though largely based on electrophysiological evidence, are logically similar to the view put forward in the 1960s by Melton (1963), who basically argued that the same functional variables (e.g., repetition effects) are operational under both short-term and long-term retention conditions, with no compelling need for separate memory systems. The similarities between the approaches of Melton and Ruchkin et al. are evident in the discussion of the fMRI findings of Prabhakaran et al. (2000), in terms of a consolidation process shared by both short- and long-term episodic memory. In this commentary I shall consider the neuropsychological evidence that counters Ruchkin et al.'s conclusion, suggesting a view of memory in terms of separate, though interacting, systems.

The electrophysiological evidence from neurologically unimpaired subjects reveals the time course of the contributions of different systems to behavioural performance. As such, it is fully adequate to reveal interaction and cooperation among systems, because this is the "normal" state. The behavioural evidence that short-term memory performance is also based on long-term memory systems, is well known (Brenner 1940; Watkins 1977). Electrophysiological and behavioural experiments in unimpaired individuals may be less likely, however, to show the independence of discrete components. Experiments in brain-injured patients typically provide this type of evidence: One single component may be selectively impaired, but the remaining parts of the system are still fully operative.

The neuropsychological evidence is mentioned in the introduction, but not further discussed in the following sections of the target-article. The main neuropsychological point raised by Ruchkin et al. concerns a case study (patient AB), reported by Romani and Martin (1999), who shows a deficit in word learning and a mild reduction of memory span, particularly for words. Ruchkin et al. state that patients such as AB "with a semantic short-term memory deficit also have difficulty forming semantic but not phonological long-term memories" (sect. 1.2, last para.), and this impairment at the lexical-semantic level of representation argues against a distinction between short-term and long-term memory. Patient AB (Romani & Martin 1999, pp. 59 and 61), however, in addition to a lexical-semantic impairment, has some deficit of phonological memory (as revealed by his low nonword span and reduced recency effect). AB's phonological learning (i.e., of novel words) was not assessed, but on the basis of the patient's mild deficit of phonological short-term memory, some impairment may be predicted (Baddeley et al. 1988). Patient AB is not, therefore, a "pure" (with a single functional deficit) case (Vallar 2000), and interpretation is more complex. With these limitations in mind, a deficit at some level of lexical-semantic representations (accord-

ing to Romani & Martin 1999, specific lexical-semantic memory resources) may account for AB's neuropsychological pattern, considering that immediate verbal-memory performance (e.g., in span tasks) has a long-term memory component. The additional inference that no independent short-term store exists, however, does not follow. For instance, AB's digit span of three and word span of two-to-three is in the upper range of the performances of short-term memory patients. In the meta-analysis by Vallar and Papagno (2002), digit span is 2.38 (range 1–3.6) and word span is 2.00 (range 1.05–3). This level of performance may reflect the combined effects of a (mild) phonological deficit and of a (more severe) lexical-semantic impairment, and is fully compatible with the view that span performance, which is mainly based on the operation of the phonological short-term store/rehearsal system, also reflects a contribution from lexical-semantic long-term memory-based representations.

Ruchkin et al. interpret the patterns of impairment of patient AB in terms of a deficit of a particular type of representation (lexical-semantic), with the short-term/long-term dimension being related only to the time course of the task, with no reference to discrete anatomo-functional components. Deficits involving specific levels of representation indeed exist, both at the phonological level (see Shallice & Vallar 1990, for discussion; Strub & Gardner 1974) and at the lexical-semantic level (Romani & Martin 1999), which may give rise to impairments in both short- and long-term memory paradigms. Here, again, Ruchkin et al. are back to the past, with a view of memory systems in terms of discrete levels of processing, each of which encompasses both short-term and long-term storage (Craik & Lockhart 1972). Levels of representation and processing are, however, articulated in a number of specific components. In the phonological domain, for instance, an anatomo-functional distinction may be drawn between a phonological short-term store and a process of rehearsal. Within the phonological domain, deficits of these systems may bring about selective patterns of impairment: Dysfunction of the process of articulatory rehearsal (but not damage to the phonological short-term store) disrupts the patients' ability to make some phonological judgements about stress position and initial sound for written words (Vallar et al. 1997). These processes have discrete anatomical counterparts (Vallar et al. 1997), revealed by neuropsychological studies in brain-damaged patients and neuroimaging-activation experiments in normal subjects (Paulesu et al. 1996). This neurofunctional architecture (Fig. 1) also provides an account of the interactive effects of the sensory modality of the input, of phonological and item-length effects, and of articulatory suppression (Vallar & Papagno 2002). The neuropsychological evidence for a distinction between short-term and long-term components is even more compelling in the visuo-spatial domain, in which double dissociations between immediate retention and long-term learning for spatial locations have been reported (Vallar 2002; Vallar & Papagno 2002).

In the schematic of the timing of stores and processes that contribute to the operations of visual and verbal short-term memory (target article, Figs. 3 and 7), the concept of distinct systems – which, however, cooperate to support optimal retention performance – is visually conveyed to the reader. The neurophysiological data reviewed by Ruchkin et al. emphasize the interactions among systems and their partly parallel activation, and the neuropsychological evidence reveals their multicomponential nature. The proper weighting of each source of evidence provides a balanced view of the multicomponent architecture of memory.

ACKNOWLEDGMENT

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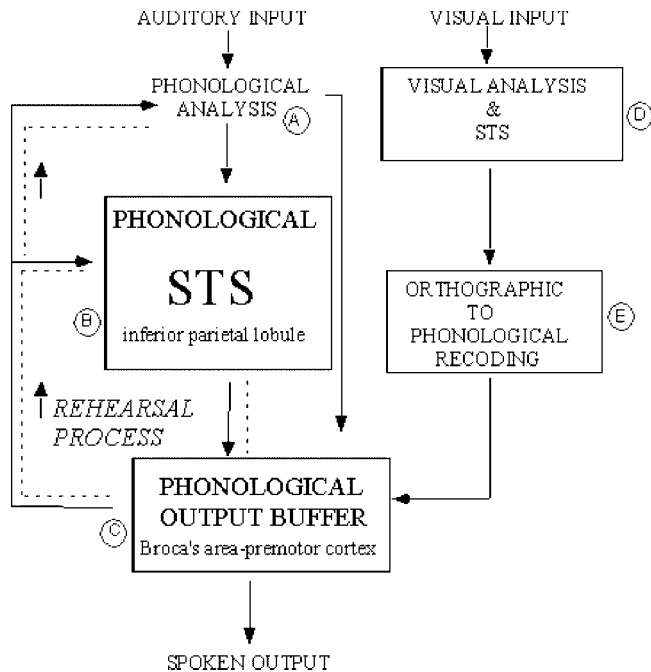


Figure 1 (Vallar). An anato-functional model of phonological short-term memory. Auditory-verbal material, after early acoustic and phonological analysis: (A) enters the main retention component of the system, the phonological short-term store (STS) (B), where material is coded in a phonological format. The phonological STS is an input system, to which auditory material has a direct and automatic access. The process of rehearsal is conceived of as involving a recirculation of the memory trace between the phonological STS and a phonological-output system, the phonological output buffer, or phonological assembly system (C), primarily concerned with the articulatory programming of speech output, with a recurring translation between input (acoustic) and output (articulatory) phonological representations. The phonological-output buffer provides access for visually presented verbal material to the phonological STS, after phonological recoding or grapheme-to-phoneme conversion (E). The model also illustrates the multiple-component nature of short-term memory, showing a visual STS (D), where material is likely to be encoded in terms of shape. (Source: Vallar & Papagno 2002).

Double dissociation in the effects of brain damage on working memory

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Abstract: As revealed by standard neuropsychological testing, patients with damage either to the frontal lobe or to the hippocampus suffer from distinct impairments of working memory. It is unclear how Ruchkin et al.'s model integrates the role played by the hippocampus.

Dissociation between two different aspects of working memory is a standard finding in my neuropsychological practice. The two critical tests are Wechsler's Digit Span and Rey's Auditory Verbal Learning Test (AVLT). Denoting an inconspicuous outcome by "+" and a pathological outcome by "-" all four possible combinations can be observed in distinct populations: ++ (both scores are normal), -- (both scores are pathological) and, theoretically most important, +- and -+, forming a double dissociation.

In the Digit Span test, the tested person has to immediately repeat series of numbers with increasing lengths, or has to reverse

the series in memory and then repeat them backwards. (Unfortunately, the current German version does not provide separate norms for forward and backward tests). In the AVLT, the same list of 15 words is read to the person five times. Each time, the person has to say immediately afterwards the words he or she remembers. The number of words remembered at the fifth presentation is the "Learning" measure, and the number of words freely recalled after being presented with an interfering list is the "Recall" measure. Norms were taken from Geffen et al. (1990) and Ivnik et al. (1992).

Figure 1 gives examples for the dissociating patterns. Not illustrated are cases where both Digit Span and AVLT yield pathological results (which occurs most often in dementia-causing illness). Rather, Figure 1a-c shows patients with relatively good AVLT performance, but severely restricted digit span, and Figure 1d-e shows patients with normal (or perhaps even compensatorily enhanced) digit span, but severely impaired learning and recall (AVLT scores).

Figure 1a is from a patient with mild sensory aphasia after infarction of the left middle artery. Digit Span was severely affected. But, nevertheless, the patient was able to learn verbal material in the AVLT. (Some verbal tests, e.g., "Similarities," and also "AVLT-Recall," were not performed because of the clinically obvious aphasic syndrome.) Figures 1b and 1c show the typical residual deficit after left frontal-lobe contusion caused by a closed-head injury: The contusion produces a bottleneck in getting information into the brain (impaired digit span), without affecting the core ability of learning and recall. Figure 1b is from a medical practitioner who, after the accident, had resumed her work but complains about difficulties in dealing with this work. Figure 1c is from an elderly man who was multiply affected by the accident, lowering his overall performance, but most severely, his digit span.

The patients in Figures 1d-e had completely intact digit span but were basically unable to learn and remember, as indicated by the AVLT scores. They had isolated, severe damage of both hippocampi, the patient in Figure 1d by simultaneous infarction of both posterior hippocampi, and the patient in Figure 1e by carbon monoxide poisoning. By this double dissociation, these cases show that, indeed, two separate systems contribute to auditory working memory. The closest interpretation of the functions of these two systems is that the first component (affected in Figs. 1a-c) contributes to a short-term buffer and that the hippocampal component (affected in Figs. 1d-e) contributes to encoding and retrieval. Elaborating on this interpretation with regard to the first component, Ruchkin et al. make the point that the frontal areas (damaged in patients, as shown in Figures 1b and 1c) might in fact not contain the short-term buffer, but rather, might provide pointers that refer to items stored in parietal areas, in this case perhaps Wernicke's area (which is directly damaged in Fig. 1a). This interpretation is in complete agreement with these neuropsychological data. However, Ruchkin et al.'s model is tacit with respect to the function of the hippocampal system. Describing and labeling the function of this system seems essential, because, as shown by the double dissociation, working memory may be severely damaged when the frontal lobes are intact and, correspondingly, damage to the frontal lobes may impair the short-term buffer but not necessarily the ability to encode and retrieve. Ruchkin et al.'s model mainly draws from event-related potential (ERP) data, and directly assessing the hippocampal contributions by means of event-related potentials might be difficult. (Cf. the discussion on assessment of the hippocampal pathology in Alzheimer's disease by means of event-related potentials in Verleger 2002.) Nevertheless, these contributions should be appreciated when modeling the function of working memory.

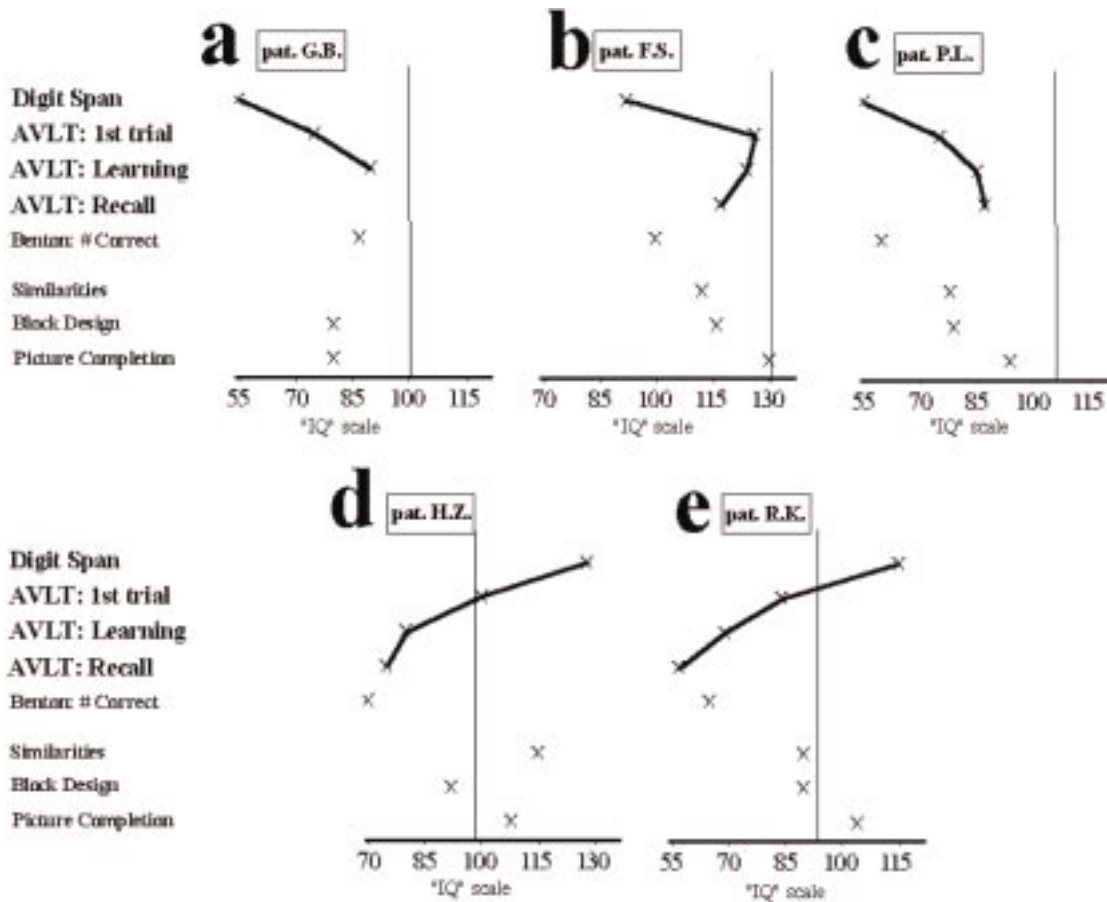


Figure 1 (Verleger). Double dissociation between memory functions measured by Digit Span and by AVLT. To have a common scale, all tests scores were converted to the IQ scale, transforming their means to 100 and their standard deviations to 15. Premorbid cognitive level, indicated by the vertical line, was estimated with a vocabulary test (Lehrl 1977), and basic aspects of cognitive functions were evaluated with the Wechsler Adult Intelligence Scale subtests: Picture Completion, Communalities, and Block Design (Tewes 1991). Benton's test of visual retention was included as an additional test of memory, but it did not clearly contribute to the double dissociation (being affected in all patients, except in Wernicke aphasia, panel a).

Neuronal synchronization accompanying memory processing

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Abstract: In their target article, Ruchkin et al. propose sustained neuronal interaction of prefrontal and posterior cortex involved in memory-storage mechanisms with respect to electrophysiological findings on the relationship of short-term and long-term memory processes. We will evaluate this claim in light of recent evidence from our laboratory on EEG coherence analysis of memory processes accompanying language comprehension.

Referring to several event-related potential (ERP) studies and one electroencephalographic (EEG) coherence study, Ruchkin et al. support the view that the same multiple memory systems serve short-term as well as long-term memory, and that only the degree of coactivation between the relevant memory systems differs. In contrast to models proposing specialized neural systems as short-term buffers, Ruchkin et al. postulate that short-term storage mechanisms involve an increase in neural synchronization during

both the encoding/comprehension and the retention phases. In particular, they propose an increased synchronization between the prefrontal cortex, serving as a top-down controlling system, and the posterior cortex, which participates in perception and encoding.

One of the few methods suitable for measuring frequency band-related neuronal synchronization accompanying cognitive processes in healthy humans is the calculation of coherence between EEG or magnetoencephalographic (MEG) signals. During the last 20 years, several cognitive processes, such as memory, language, music processing, and thinking, have been studied with EEG coherence (for reviews, see Petsche & Etlinger 1998; Rappelsberger & Petsche 1988). Consistent with Ruchkin et al.'s results on EEG coherence accompanying memory processes, increased neuronal synchronization, in particular between signals at distant electrodes (large-scale coherence), was described for various different, complex cognitive tasks (for reviews, see Bressler & Kelso 2001; Petsche & Etlinger 1998). Other measures, such as phase synchronization (Varela et al. 2001) or phase relations (Schack et al. 2003), which indicate direction and propagation speed of information transfer, are even more promising for investigating large-scale synchronization. In general, high coherence correlates with long-lasting negativities in the ERP and is often found during increased task complexity and efficient information processing, whereas low coherence is often found in pathological conditions (for reviews, see Petsche & Etlinger 1998; Weiss & Mueller 2003).

In an EEG coherence study, Ruchkin et al. found increased theta coherence (4–6 Hz) during sentence comprehension, but not during retention. The reverse was true for the 10–14 Hz band. These frequency-specific results partly correspond to our findings on EEG coherence changes in an experiment where subjects process English relative clauses (Weiss & Mueller 2003; Weiss et al. 2001). Within the theta band (5–7 Hz), more complex relative clauses showed significantly higher coherence in the post-relative clause, whereas within the beta-1 band (13–18 Hz), they already showed higher coherence at the beginning of the relative clause and in the post-relative clause. One of the possible interpretations of these findings is that theta activity is related to working memory and that beta-1 correlates to the activation of a separate parsing buffer, similar to that proposed by Caplan and Waters (1999). This means that, at the beginning of the relative clause, the load of the parsing buffer significantly differs between the two sentence types, whereas the load of working memory does not significantly differ at this stage. Another possibility is that the beta-1 band reflects syntactic working memory and theta is correlated with efficient processing during verbal memory encoding. This may partly explain Ruchkin et al.'s present results. Although these questions have to remain open at present, coherence within different frequency bands possibly reflects different aspects of sentence processing (Weiss & Mueller 2003; Weiss et al. 2001).

The finding of Ruchkin et al. on increased neuronal large-scale synchronization during memory processes corresponds well with our findings on EEG coherence during memory encoding of words (Weiss & Rappelsberger 2000; Weiss et al. 2000). In these studies, nouns – later successfully recalled – exhibited overall enhanced synchronization but showed typical patterns, especially between left frontal and posterior sites. This increased neuronal synchronization occurred regardless of modality (auditory or visual material) and word category (concrete or abstract). In addition, the degree of interhemispheric synchronization was higher during encoding of later-recalled nouns, suggesting an increased hemispheric interaction. In order to avoid detecting strictly linear dependencies, and because coherence concerns correlation across trials of both amplitude and phase, phase synchronization was also calculated (Schack & Weiss 2003). Differences in evoked and induced-phase synchronization for recalled versus non-recalled nouns appeared for theta, alpha, and gamma oscillations. Gamma oscillations at *Fz* and *Cz* were nested in theta oscillations for recalled nouns. Recently, Schack et al. (2002) found increased phase coupling of theta-gamma EEG rhythms during short-term memory processing by means of bispectral analysis, suggesting an amplitude modulation of gamma frequencies by slow oscillations. The pattern of anterior–posterior EEG coherence and phase synchronization accompanying verbal memory encoding allowed us to assess the probability of whether nouns would be recalled or not.

Ruchkin et al.'s findings and our results argue that EEG-coherence analysis is an important tool for studying high-level cognitive processes, such as language or memory. This method supports a somewhat different view on brain function, insofar as the actual information processing is not correlated with location, but with interaction. With the calculation of coherence, it is also possible to get information on the temporal dynamics during cognition with the same temporal resolution as with ERPs (Schack et al. 2003). In addition, coherence is a frequency-dependent measure, and patterns of coherence networks tend to differ between frequencies. The meaning of coherence networks may be interpreted differently depending on the frequency band investigated, because different components of a cognitive task are presumably processed via different frequencies (Basar 1998). During linguistic information processing, our own studies point at different roles of high- and low-frequency synchronization. Activities within the theta frequency range (around 3–7 Hz) seem correlated with language-related mnemonic processes, and theta coherence increases if task demands increase and more efficient in-

formation processing is required. The alpha frequency (8–12 Hz) is probably important for sensory and, in the higher range, for semantic processing, whereas the beta (13–30 Hz) and gamma (>30 Hz) frequencies seem to be correlated with more complex linguistic sub-processes, such as syntax or semantics (for a review, see Weiss & Mueller 2003). Large-scale information transfer via frequency coding is possibly one of the mechanisms that facilitate parallel processing within the brain, since a single signal may contain different aspects of information within various frequency ranges.

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Authors' Response

Working memory: Unemployed but still doing day labor

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Abstract: The goal of our target article is to establish that electrophysiological data constrain models of short-term memory retention operations to schemes in which activated long-term memory is its representational basis. The temporary stores correspond to neural circuits involved in the perception and subsequent processing of the relevant information, and do not involve specialized neural circuits dedicated to the temporary holding of information outside of those embedded in long-term memory. The commentaries ranged from general agreement with the view that short-term memory stores correspond to activated long-term memory (e.g., **Abry, Sato, Schwartz, Loevenbruck & Cathiard** [Abry et al.], **Cowan, Fuster, Grote, Hickok & Buchsbaum, Keenan, Hyönä & Kaakinen** [Keenan et al.], **Martin, Morra**), to taking a definite exception to this view (e.g., **Baddeley, Düzel, Logie & Della Sala, Kroger, Majerus, Van der Linden, Collette & Salmon** [Majerus et al.], **Vallar**).

We first discuss comments on the scope of the target article and respond to questions raised about the utility and validity of event-related potential (ERP) data in the study of short-term memory. We then address neurophysiological data that appear to contradict the contention that activated long-term memory is the representational basis for short-term memory, followed by a discussion of neurophysiological data presented in the commentaries that support the contention. We then address misinterpretations of our position, the issue of activation of long-term memory in the processing of novel information, and briefly comment on sleep and memory consolidation.

R1. Scope of the target article

Regardless of the degree of agreement or disagreement, the target article has been commonly criticized for incompleteness; for not providing a comprehensive, completely specified model of memory, and/or not considering all of the neural systems that contribute to short-term memory operations. Some of these omissions were deliberate. It was not our intention to develop another model of “working memory.” Rather, we restricted ourselves to making the case that models of short-term memory retention operations should be based upon temporary stores consisting of activated long-term memory, and that modeling should take neurophysiological data into full account. We do not think that enough is known at this time to present a completely specified model of short-term memory. The target article provides an indication of some of the directions that memory research needs to take to specify such a model.

Logie & Della Sala object to the contention that short-term memory representations are constituted by activated long-term memory, stating that it fails to account for the combination of on-line processing and temporary memory storage posited by Baddeley’s model of “working memory.” These commentators argue that a theory postulating separate short-term and long-term memory stores is more readily tested by behavioral data. However, no compelling explanation or evidence is provided for these opinions. Rather, Logie & Della Sala observe that a theory of short-term memory based on activated long-term memory would have to make a wide range of assumptions about the neurophysiological properties of the activation process, which we did not do. Note that the separate short-term stores postulated in Baddeley’s model of “working memory” also require a wide range of assumptions about their neurophysiological properties, especially concerning the neural implementation of their codes. In any event, neurophysiological properties should not be assumed, but should be established by empirical studies. Theories should not be confined to simply being readily testable by behavioral data. Behavioral data are necessary, but not sufficient, for a full understanding of the structure and operation of memory.

We limited ourselves to primarily discussing neural systems that were most clearly indexed by our ERP data. Although not essential for our argument, further mention of other neural systems might have been helpful, and thereby spared readers **Heil, Rösler & Rolke’s** (**Heil et al.’s**) polemic decrying our not presenting a complete theory of memory. We are most appreciative of the **Cowan** and **Jonides & Awh** commentaries, which provide a more complete account of the structures that participate in focusing of attention and controlling short-term memory operations, pointing out that parietal cortex, as well prefrontal cortex, is involved. We did not intend to imply that the long-term memory stores underlying short-term memory operations are confined to posterior cortex. The position that we hold, but failed to make explicit, was insightfully and eloquently expressed in **Fuster’s** commentary, that “the activation of long-term memory is essential to the processing of *all* cognitive functions,” with long-term memory being the *structural* basis for these functions. As mentioned in the conclusion of the target article (sect. 5), there are long-term stores in frontal cortex for motor programs, scripts, attentional control programs, and social and goal-oriented behaviors. Their activation also contributes to the functioning of

“working memory.” Limiting our mention of prefrontal cortex to aspects that are directly involved in refreshing activation of long-term memory representations was not intended to imply that prefrontal cortex did not have other crucial information processing roles, as succinctly detailed in the **Ryan & Cohen** commentary. A fuller account of our views on the roles of prefrontal and posterior cortex is provided in Wood and Grafman (2003).

Barceló, Periáñez & Gomila (**Barceló et al.**) comment that we have not dealt with supraordinate memory. They summarize the results of an experiment in which task rules could change from trial-to-trial, and elicited ERPs with phasic deflections sensitive to whether or not a rule change was required, and the number of rules held in memory (Barceló et al. 2002). The ERP deflections evidently indexed updating, maintaining, and transforming of information, operations associated with supraordinate memory. The deflections were distributed across scalp regions overlying frontal and posterior association cortices. Barceló et al. argue that the ERPs reflected, in part, the action of long-term memory networks that were engaged for the rapid retrieval of new task rules. This fits well with the broader framework for the role of long-term memory in cognition postulated by **Fuster**. Long-term memory structures may be briefly mobilized to high levels of activation with momentary information-processing demands. The level of activation then decays as operations that meet the processing demands are completed.

Maybery, Parmentier & Clissa (**Maybery et al.**) remark that we did not present well-specified mechanisms for retention of serial order, binding, or the control of attention. While we have no quarrel with their general views on sequencing, Maybery et al. need reminding that timing of items at presentation could be relevant, depending on the stimuli used and the response required (e.g., script vs. word level, or cascading presentations and a stimulus timing decision based on a duration estimate). We agree with Engel and Singer’s (2001) emphasis on the importance of binding and have discussed it elsewhere (Grafman & Weingartner 1996). The mechanisms for binding should include synchronous activity that ensures cotemporal activation for the strengthening of representations, but that was not the point of our target article.

With regard to the control of attention and the prefrontal cortex, Wood and Grafman (2003) nicely summarize the representations in the prefrontal cortex that influence lower level representations and processes. The prefrontal cortex representations are subject to the same rules that govern nonfrontal representations. We agree with **Osaka** that the prefrontal cortex biases and coordinates with the posterior brain, and that the posterior cortex provides the representations for short-term memory operations. We are inclined to agree with **Elliott, Conci, & Müller’s** (**Elliott et al.’s**) argument that synchronization of prefrontal and posterior cortex is involved in the formation of stimulus-related persistence.

R1.1. The hippocampus and binding

The **Foster** and **Verleger** commentaries noted that we had little to say about the hippocampus. In reply to Foster’s query, it is difficult to investigate medial temporal lobe operations with methodologies based on scalp-recorded ERPs. Hence, we did not offer ERP data delineating hip-

pocampal operations. Foster raises questions concerning the role of the medial temporal lobe system in our view of short-term memory, in particular with respect to our contention that short-term episodic memory consists of well-consolidated and partially consolidated long-term memories in an active state. Foster notes that the conventional consolidation hypothesis posits that memories are “downloaded” to the neocortex. Our view is that binding processes under the control of hippocampal-neocortex connections are responsible for inducing simultaneous activations across long-term stores that lead to an episode being stored (Rickard & Grafman 1998).

We briefly argued in the conclusion (sect. 5) that a key function of the hippocampus is to bind together, in time, representations that may differ in kind (e.g., objects and context), time duration (e.g., words and plans), and other characteristics. This binding mechanism serves to create a complete episode in memory and aids in the slow and deep consolidation of representational knowledge over time via associative links (i.e., episodes) that are reactivated during thinking and retrieval (Davachi & Wagner 2002). In our view, lesions to the hippocampus and related structures cause a profound inability to create new episodes (amnesia), because of a binding deficit, and, to a lesser degree, deprive the amnesic patient of one prominent mechanism that aids in the strengthening of stored memories.

Knowlton & Viskontas challenge our argument that a binding deficit is the best explanation for amnesia. They use two counter-examples against our argument: an observation of impaired context-free semantic learning in amnesics and a reverse temporal gradient seen in some patients with semantic dementia. These two counter-examples raised by Knowlton & Viskontas stand out against a tide of animal and human studies suggesting the critical role of the hippocampus and related structures in binding disparate information together to form an episode (Eichenbaum 2000). There is also substantial evidence that humans spontaneously and effortfully search through their memory for various purposes regularly, and those searches re-activate semantic representations stored earlier via associative links – some of which come from episodes (Schacter & Buckner 1998). Amnesics can search their memory for episodes and other information encoded before the onset of their amnesia, but are severely limited in using such searches to re-voke postamnesic episodes, and, instead, must depend upon environmental cues and stimulation to re-voke post-amnesic episodic memories (Kopelman 2002). Amnesics, therefore, can show improved procedural and implicit memory when stimuli are provided as cues for their responses. (Typically in these tasks, subjects are not asked to explore their memory, but simply name an object or word or press a response key whenever a target appears; Speirs et al. 2001.) It is not clear that this kind of “surface feature” priming requires binding at all, as none of the usual conditions for episodic binding apply (who, what, where, and when). Rather, this kind of priming is simply a strengthening of the individual unbound representations.

Not all amnesic patients demonstrate fact-learning ability, but there are individual differences in the degree of hippocampal damage in, for example, anoxic and encephalitic patients, which might permit some new learning – albeit greatly reduced compared to normal controls. In addition, the route used for retrieval of this factual information could

very well be based on the surface features of the stimulus, rather than some associative or conceptual learning mechanism. Amnesics can demonstrate new learning, but they have great difficulty binding and later remembering the context in which the new learning took place. Regarding semantic dementia, we want to stress that, without an autopsy, it is unclear whether patients receiving a provisional clinical diagnosis of semantic dementia have the pathology or a variant of frontotemporal dementia, Alzheimer’s disease, or another dementia. Too few cases have come to autopsy for a definitive clinical test(s) or diagnostic schema to be developed. This is not a trivial issue, since the hippocampal involvement in these patients may differ, depending on the underlying pathology (Laakso et al. 2000).

In any case, we will assume that episodic memory is spared in the semantic dementia patients referred to by **Knowlton & Viskontas**, even though their semantic knowledge is affected. We don’t see how this counter-example diminishes our argument. In semantic dementia, as described by Knowlton & Viskontas, binding should be relatively intact, whereas some of the subcomponents of binding that concern semantic knowledge would be degraded. The act of recognizing famous people, without access to autobiographical knowledge about them, would be a behavior that reflects a binding mechanism bereft of some of the subcomponents of knowledge that are usually part of the episode, and requires no special explanation within our framework. Recent memories for faces that are famous could simply be an exposure effect – greater exposure to currently famous faces and names rather than to famous faces and names from the past. Since fewer words or objects would be subject to the same exposure bias (i.e., new vocabulary or objects appear slowly throughout life and their common use is not limited to the generations in which the new words or objects appear concurrently), an exposure effect would be more likely to be seen with things that have varying media exposure and are not limited to a specific generation, such as television, movies, newspapers, and conversations. Moreover, amnesia doesn’t impair all types of binding, as amnesics, for example, are not agnostic and can perceive and use objects – this functionality requires the cortically-local binding of a number of visual features together in order for the person to “know” the object. Amnesia more likely affects binding that occurs across a longer-scale time window. A lack of binding would technically not impair semantic memory mechanisms, but since semantic memory would no longer benefit from episodically derived spontaneous retrieval of recently exposed information, as we noted above, the strengthening of information across time would be diminished, and the number of new associative links would also be limited. Thus, semantic memory would be indirectly affected in amnesia, but semantic representational mechanisms should remain intact.

Grossberg comments that our view of the linkage between short-term and long-term memory conflates their different roles. He uses an example where the words MY and SELF have been learned, and the word MYSELF is stored in “working memory” for the first time. Grossberg seems to imply that, in our framework, the representation for MYSELF would overwrite the representations for MY and SELF. This is contrary to our view, which is that a new binding would be established between MY and SELF.

R1.2. Processing and retention of sentences

Friederici & Bornkessel criticize the target article's treatment of sentence comprehension, in the section entitled "Sentence processing and semantic relatedness" (sect. 3.7), as being "unnecessarily sparse – at least for the domain of sentence processing." The central objective of this section was to demonstrate that semantic relationships during stimulus presentation influence mnemonic activity in a subsequent retention interval, thus providing further evidence of semantic codes making an active contribution to the short-term maintenance of verbal material. We revisited a question previously investigated by Baddeley (1966a; 1966b) and Baddeley and Levy (1971), as to why semantic similarity in word lists had only a small deleterious effect upon short-term memory performance in comparison with the effect of phonological similarity. Baddeley and Levy suggested "that the absence of semantic similarity effects in most short-term memory studies is due to the difficulty of semantically encoding unrelated words." Consequently, we reasoned that sentences, rather than word lists, would be more appropriate stimuli for studying this issue. Semantic similarity effects during retention, rather than on-line sentence processing, was the motivating issue for this section.

The use of sentences provided an apt opportunity to compare brain activity recorded during stimulus processing with that recorded in the poststimulus retention interval. Our approach was to use dipole source waveforms obtained from source analyses of the scalp ERPs. The waveforms from the source analysis of the ERPs, elicited by sentences with semantically unrelated nouns (Fig. 10 of the target article), exemplified the results. Both **Grote** and **Friederici & Bornkessel** expressed interest in the source waveforms for the ERPs elicited by the related nouns. The timing and pattern of deflections of the source waveforms for the related nouns closely resembled that of the source waveforms for the unrelated nouns presented in Figure 10. There were some differences in amplitudes, most markedly for the left and right temporal gyrus waveforms in the postsentence retention interval. This difference between source waveforms corresponded to the reduction in the postsentence sustained negativity, observed at posterior scalp sites for the ERPs elicited in the unrelated nouns condition, in comparison with the ERPs elicited in the related nouns condition.

Friederici & Bornkessel's assertion, that the right temporal gyrus source waveform "increases its activation systematically" only during retention, is better expressed as "it displays tonic activation" only during retention. Note that the right temporal gyrus source waveform displayed systematic phasic activation during sentence processing (Fig. 10, target article). **Friederici & Bornkessel's** alternative interpretation of the hemispheric differences between temporal gyri source waveforms during sentence processing is plausible, that is, on-line sentence processing requires more syntactic resources, which are located in the left hemisphere. However, it is more likely that the hemispheric difference resulted from the combination of the left hemisphere providing both more syntactic resources and finer grain semantic processing. Analyses of the ERP and EEG activity during sentence presentation indicated that there was semantic as well as syntactic activation (Haarmann et al. 2002; 2003a). Thus, **Friederici & Bornkessel's** observation, that more syntactic processing is required during sen-

tence comprehension than during retention, presents no problems for our interpretation that sentence comprehension and short-term retention of meaning involve the same, or very closely located, posterior neural regions. If syntactic representations activated during stimulus processing are not needed during retention of meaning, then their activation need not be sustained. However, the activation of semantic representations necessary for the retention of meaning will continue to be sustained in the postsentence retention interval.

In response to **Grote's** query, the age of most of the participants in our experiments was in the early twenties to mid-thirties range. The participants were paid volunteers recruited mainly from the University of Maryland, Baltimore community. They were primarily either graduate students, medical students, postdoctoral fellows, or laboratory technicians, usually with over 16 years of education. There was overlap among the cohorts in the various studies, but the cohorts were not identical.

R2. Utility and validity of ERP data

Baddeley expresses a concern for what he terms the correlational fallacy, that is, the assumption that if ERP activity coincides with short-term memory operations, then such activity is responsible for the observed behavior. Neither we nor most investigators who use ERPs as dependent variables make such assumptions. ERPs are used as indicators of the state of brain activity in a specific time interval, thereby providing a means of observing covert mental processes that may not be readily apparent in behavioral data. The functional significance of a particular ERP phenomenon depends upon how it responds to manipulations of experimental conditions. In studies of short-term memory, when a particular ERP deflection is shown to be influenced by the properties of stimuli presented well before the deflection, then it can be concluded that the ERP deflection is an index of brain activity associated with mnemonic processing of the stimuli. For example, the ERP activity recorded during retention of verbal material that was either heard or read (sect. 3.1) was sensitive to both the modality of the preceding stimulus (see Fig. 4a of the target article, sect. 3.1) and memory load, the number of syllables in the preceding stimulus (Ruchkin et al. 1997). For our purposes, the effects upon poststimulus ERP activity resulting from manipulating the properties of previously presented stimuli provided information on the types of codes that were active during the retention interval. Such information cannot be conclusively obtained from behavioral responses.

As an example of the purported correlational fallacy, **Baddeley** uses the effect of visual versus auditory presentation of verbal material upon ERP activity, recorded during retention of the verbal material (sect. 3.1, Fig. 4a, target article). **Baddeley** argues that, since stimulus modality has a large effect upon the ERPs, while having only a limited effect upon task performance, the differences in ERP activity were not likely to be closely linked to task performance. Hence, our interpretation of the data is a correlational fallacy. **Baddeley** seems to have missed the point that even when task performance does not vary as a function of the conditions under which the task is performed, relevant brain operations may vary (which may be why task perfor-

mance is held constant in the face of varying conditions). That there was little difference between task performance for material that was heard or read does not mean that mnemonic brain operations were the same for the two modalities. Achieving near identical levels of accuracy when performing a task under different conditions can require that the brain activity underlying task performance differs as a function of the conditions. A problem with trying to avoid supposed correlational fallacies is that it leads to ignoring a vast body of important neuroscientific data.

Taking the argument of accessing covert brain processes further, the data in Figures 8 and 9 (sect. 3.6) are an example of ERPs serving as probes into the nature of mnemonic brain mechanisms. Task performance was not an issue. Rather, the ERPs were used as measures of the activation level of semantic long-term memory.

What all this means is that behavioral measures are blunt instruments that cannot sense all that is happening in the brain. The brain has far more degrees of freedom than can be captured by the tip of the finger or by spoken or written responses. Converging information from other blunt instruments, such as lesion data, electromagnetic measures, and hemodynamic imaging, are also needed for the formulation of a more complete and ultimately accurate model of short-term memory.

Logie & Della Sala comment on the issue of subject choice in selecting strategies for the performance of a task. They cogently point out that if this is not suitably controlled, then the result could be the mapping of tasks, instead of cognitive functions, onto brain activity. The imprecision of such results would negate their value for constraining theories. We have dealt with this problem by initially constricting subjects' strategies via instructions and practice, and then extensively debriefing subjects at the end of the experimental session, a strategy rarely used by proponents of separate short-term and long-term memory stores.

In the final paragraph of their commentary, **Logie & Della Sala** focus on the sentence-processing and retention data described in section 3.7 of the target article, upon which we based our argument for proceduralism. They attribute to us the view that "activation of the same brain areas indicates that the same cognitive function is involved" (para. 4). That is not what we said. Our ERP data indicated that the same brain area can be engaged in different cognitive operations at different times. Specifically, the data in section 3.7 showed that posterior temporal regions were active: (1) during sentence presentation on a phrase-by-phrase basis when stimulus acquisition and comprehension, bottom-up processing, were predominant, and (2) after sentence presentation was complete on a sustained basis when retention, top-down processing, was predominant. These results are an example of encoding and subsequent retention operations involving the same brain region.

Logie & Della Sala point out that prefrontal areas are also active during retention, and that "temporary memory appears to be associated with both anterior and posterior areas of activation" (last para.). There is widespread agreement on this point. **Logie & Della Sala** have considered three interpretations of these data: (1) prefrontal memory is the seat of short-term memory; (2) both prefrontal and posterior activation are required; (3) prefrontal activation reflects controlling mechanisms that continue the maintenance of long-term memory traces. The second and third interpretations, with which we agree, overlap in the sense

that the third interpretation implies the second interpretation. **Logie & Della Sala** conclude that, at a conceptual level, the three interpretations are consistent with "working memory" comprising a system that is conceptually quite distinct from long-term memory.

Although the "working memory" system and long-term memory can be viewed as conceptually distinct, the target article is not concerned with that issue. We are concerned with one aspect of the "working memory" system, namely, the neural implementation of short-term storage. Long-term memory is a structure, embodied in the vast arrays of connections among neural circuits. Short-term memory, we believe, is a process that results from activation of the long-term memory structure. Long-term memory is the structural basis of what **Logie & Della Sala** call the mental workspace. Short-term memory processes contribute to the functioning of the mental workspace. While it can be said that "working memory" and long-term memory are distinct conceptually, it can also be said that the short-term storage components of "working memory" are not structurally distinct from long-term memory.

R3. Neurophysiological challenges

Düzel questions the use of ERP data in the study of short-term memory, noting that there is only a limited understanding of the basic neural mechanisms underlying cognitive operations; and he states that it is difficult to conclude, from the available data, the nonexistence of distinct specialized short-term memory stores. Our position is that, in principle, it is not possible to prove that a hypothesized phenomenon, such as specialized temporary stores, does not exist. The failure to obtain compelling evidence for such temporary stores, in combination with compelling evidence for an alternative temporary storage mechanism, is the most that can be done. The convergence of available data and the principle of parsimony combine to favor the activated long-term memory hypothesis, rather than the topographically distinct specialized buffers hypothesis.

Düzel claims that a study by Chafee and Goldman-Rakic (1998) provided evidence that prefrontal cortex neurons temporarily store stimulus information, because Chafee and Goldman-Rakic found that neurons in prefrontal and parietal cortex of monkeys displayed similar (but not identical) sustained activity during the retention interval of a delayed saccade experiment. However, that was not Chafee and Goldman-Rakic's conclusion. They cautioned that similarity of the physiological properties of neurons in different cortical regions does not necessarily indicate a functional equivalence, but rather may be a reflection of mutual connectivity and coding. Note that such connectivity is a necessary property of the postulated attentional pointer system.

Finally, **Düzel** cites the results of transcranial magnetic stimulation (TMS) studies, in which TMS was applied either early (close in time to stimulus encoding) or late (during retention) in short-term memory tasks. In a study of object and spatial visual short-term memory, Oliveri et al. (2001) applied TMS at various delays over either posterior scalp (parietal or temporal) or frontal scalp (targeting either the superior frontal gyrus or the dorsal lateral prefrontal gyrus). Oliveri et al. found that TMS over posterior scalp caused slower response times (RTs) when the TMS was

close in time to stimulus presentation, and had no effect upon behavioral performance when late in the retention interval. In contrast, impaired responses resulting from TMS over frontal scalp only occurred when the TMS was late in the retention interval. TMS directed at the superior frontal gyrus caused slower RTs in the spatial task, whereas TMS directed at the dorsal lateral prefrontal gyrus caused slower RTs and reduced accuracy in both the spatial and object tasks. Düzel claims that such results are compatible with frontal cortex acting as a short-term store and posterior cortex acting as an initial processor. However, that was not Oliveri et al.'s conclusion. They pointed out that the TMS directed at the superior frontal gyrus in the spatial task could have disrupted motor preparation rather than mnemonic neural activity. In view of the finding that both spatial and object tasks were impaired by TMS directed at the dorsal lateral prefrontal gyrus, Oliveri et al. interpreted the role of this region as being necessary for general, amodal "working memory" control computations. With respect to the effects of TMS over posterior regions, when TMS was applied at about the time of encoding, it only produced a slowing of RT; accuracy was not impaired. The null effect of TMS during retention may have come about because, once the stimulus material had been encoded and its representations were maintained by an attentional control drive from the frontal cortex, a level of TMS that only slowed task performance when applied during encoding, would not impair task performance when applied under post-encoding maintenance conditions.

In contrast with Düzel's view of posterior cortex only performing initial processing and frontal cortex providing temporary storage, an event-related fMRI study by Postle et al. (1999) indicated that prefrontal cortex provided control functions and posterior sensory processing areas functioned as short-term stores. Postle et al. manipulated both the amount of material to be maintained in memory and the complexity of operations performed on the material held in memory during a 12-sec delay interval. They found that during the delay interval posterior cortex was primarily sensitive to the memory load manipulation, indicating a storage function, while prefrontal cortex was primarily sensitive to the complexity of the operations, indicating an executive control function. Furthermore, the results of a neuroimaging study by Kroger et al. (2002) suggest that, as the representations bound together in short-term memory increases in complexity, but not as memory load increases, more anterior regions of prefrontal cortex are recruited.

Mecklinger & Opitz question whether sensory processing regions in posterior cortex participate in the short-term memory retention process. An event-related fMRI study of visuospatial "working memory" (Mecklinger et al. 2000) failed to find evidence of sustained activation in the ventral path of the extrastriate visual system (inferior temporal cortex) during retention of visual object information. Sustained activation was found in the inferior parietal sulcus, a posterior multisensory integration area. Consequently, Mecklinger & Opitz argue that sustained activation during retention does not occur in posterior brain systems, such as the inferior temporal cortex, that are assumed to be involved in lower-order perceptual functions. Rather, Mecklinger & Opitz argue that mnemonic maintenance depends upon sustained activation in the posterior cortex, where higher-order memory representations are processed, which they assume to be a function of the inferior

parietal cortex. The conclusion that the inferior parietal sulcus was activated during retention was well supported by Mecklinger et al.'s data, but the data did not delineate in detail the functional role of inferior parietal sulcus activation during short-term retention. It may well be that its contribution was more in the domain of focusing attention during temporary storage, as discussed in the **Cowan and Jonides & Awh** commentaries.

The apparent lack of activation in the inferior temporal cortex during retention is problematic. It is a null result that runs counter to converging evidence from a number of hemodynamic and ERP studies of visuospatial "working memory." **Mecklinger & Opitz** astutely point out the limitations of the hemodynamic studies: low temporal resolution and the use of block designs that make identification of retention-related activation difficult. Although our ERP study (see target article, sect. 2) did have the necessary temporal resolution, its spatial resolution was coarse. However, given what is known about ERP source localization errors (see the Appendix of the target article and Miltner et al. 1994), it is unlikely that the sustained ERP activity attributed to activation in the ventral path of extrastriate cortex was actually a result of activation in the inferior parietal sulcus.

Mecklinger et al. (2000) used an ingenious paradigm that thoroughly controlled for differences between control and experimental conditions during encoding of the stimuli. Their approach was to require that the subject retain the same stimulus information in both experimental and control conditions during a 4-sec preliminary delay interval. The preliminary delay interval ended with a 500-msec visual cue that specified what stimulus information, if any, should be retained during and immediately following the second delay interval (also 4 sec). In the experimental conditions, subjects continued maintenance of stimulus information in the second delay interval, while in the control condition retention was discontinued. Cue properties were essentially identical in the experimental and control conditions. Thus, differences between experimental and control conditions in the neural activity during the second delay interval would be due to sustained short-term memory maintenance operations alone, since the preceding encoding operations did not vary across conditions. Because of hemodynamic delay, the hemodynamic responses were measured in a 4-sec interval starting at the end of the second delay interval.

The hemodynamic response to the visual cue stimulus, in combination with the relatively short second delay interval, may be the key to reconciling the null results of Mecklinger et al. (2000) with the positive results from other studies of visuospatial "working memory." It is likely that perception of the visual cue elicited a hemodynamic responses in the extrastriate visual cortex, which persisted into the interval in which the hemodynamic response measurements were made. Since the memory demand of the cue was relatively low, it may have elicited relatively little or no activation in the other retention-sensitive cortical regions identified by Mecklinger et al. (2000). Because the design was such that the hemodynamic responses to the visual cue were likely to have been essentially the same in the experimental and control tasks, it therefore would have been difficult to detect between-task differences in the hemodynamic responses measured in the inferior temporal cortex.

Hickok & Buchsbaum's commentary is a counterpoint

to **Mecklinger & Opitz**. Hickok & Buchsbaum observe that the well-known phenomenon of interference with serial recall of verbal material by presentation of irrelevant acoustic information implies that maintenance of verbal material involves the same region that is involved in perceptual processing of acoustic information. Hickok & Buchsbaum describe the results of two fMRI studies of this issue. Suitably long retention epochs (15–27 sec) were used in tasks that required retention of acoustically presented verbal information. The bilateral superior temporal sulcus and the left posterior superior temporal gyrus were responsive during both perceptual and rehearsal phases. The superior temporal gyrus regions correspond to areas involved in auditory speech perception and comprehension (Hickok & Poeppel 2000). Hence, their activation in both encoding and retention phases support both the idea of proceduralism and the proposition that short-term verbal memory involves activation of basic representations and their processing systems.

R4. ERP data consistent with the activated long-term memory hypothesis

Rösler & Heil criticize our use of spatial-temporal source analysis for interpreting scalp ERP data. They note that, because of the inverse problem, source analyses do not produce unique solutions, implying that we could not reliably distinguish between posterior and prefrontal sources. We have reviewed this issue in the Appendix of the target article, noting that the average magnitude of source location errors is approximately 1.4 cm, which is more than adequate for distinguishing between sources located in prefrontal and posterior cortices. Rösler & Heil further state that our topographic data did not closely link short-term and long-term memory. This is true, because the topographic analyses were primarily directed at other issues, such as whether there are multiple pathways for short-term retention of visuospatial information, different pathways for short-term retention of verbal information that is heard or read, and whether lexical-semantic representations are activated during short-term memory operations.

Rösler & Heil have then modestly offered some of their ERP topographic data as a better link between long-term and short-term memory than the data presented in the target article. The gist of Rösler & Heil's approach has been to show, for a specific type of information, a congruency of scalp topographies associated with storage, retrieval, and manipulation of the information. They argue that their data strongly supports the view that short-term memory is activated in the same cortical areas where long-term memories are stored. We are inclined to accept their results, but with enthusiasm that is tempered by methodological problems with the Rösler & Heil studies. One problem is that suitable statistical analyses, such as a power analysis or confidence limits, are needed to substantiate Rösler & Heil's claim that the topographies are indeed congruent. A second problem is that, while it is possible to conclude that different combinations of brain regions are activated when ERP scalp topographies differ, one cannot be certain that the same brain regions are activated when ERP scalp topographies are congruent. This is an aspect of the non-uniqueness of inverse solutions noted by Rösler & Heil in their critique of ERP source analysis.

When using scalp-recorded ERPs, functional approaches are more likely to be fruitful than topographic approaches to the issue of activated long-term memory as the basis for short-term memory. Our key study of this issue was presented in the "Activation of long-term memory and retention" section of the target article (sect. 3.6). Rather than attempting to show a congruence of topographies that would require accepting a null hypothesis, we focused upon differences in amplitude variations of an ERP deflection (N400) that indexed the level of activation of long-term memory and involved the more readily realized statistical procedure of rejecting a null hypothesis.

R5. Supportive EEG coherence data and inner direction of attention

The **Klimesch & Schack** and **Weiss & Mueller** commentaries give further substance to our claim that synchrony among brain regions changes as processing of sentences evolves from bottom-up encoding and comprehension to top-down retention of meaning (see Fig. 11, target article, sect. 4.2). Of particular interest for our topic was that, during retention, EEG recordings from scalp regions overlying prefrontal and frontal cortex became more highly synchronized in the 10–14 Hz band with recordings from scalp regions overlying posterior cortex. Although not reported in the target article, EEG power in the 10–14 Hz band increased markedly during retention in recordings from scalp overlying prefrontal cortex, lateral parietal cortex, and occipital cortex. These commentaries also note increased EEG activity and synchrony in the 10–14 Hz band during maintenance operations. However, increased 10–14 Hz activity during retention presents a paradox, because EEG in the 10–14 Hz band has conventionally been associated with mental inactivity (cortical idling). To resolve this paradox, Cooper et al. (2003) and Klimesch (1999) have suggested that 10–14 Hz band activity indexes the inner direction of attention, away from external stimuli, by inhibiting transmission and perception of sensory information. Such an inhibitory mechanism would help the brain go into a cortical idling mode during periods of mental inactivity. However, the same mechanism could facilitate the maintenance of mental representations within the focus of awareness by limiting processing of potentially distracting external stimuli.

R6. Misinterpretations

Patterson & Rypma mistakenly interpret a single representational basis for short-term and long-term memory as being a unitary memory system. However, a single representational basis framework is no more unitary than multiple stores "working memory" models. A single representational basis does not preclude divisions of memory along the lines of category, domain, modality, and process. Patterson & Rypma argue against the single representational basis framework by drawing upon the conclusions of some prior studies.

Shallice and Warrington concluded from their studies of a patient, KF, (Shallice & Warrington 1970; Warrington & Shallice 1969) that there were separate short-term and long-term memory systems. However, they did not take the nature of the representations into account. The short-term

memory tasks tested the phonological system, whereas the long-term memory tasks tested the semantic system. Shallice and Warrington's results did indicate that the representational bases for these two systems are different, but, despite Shallice and Warrington's intention, the issue of whether the long-term and short-term memory representational basis differs within each system was not addressed by their studies. In order to do so, both short-term and long-term memory tests should have been constrained to either only phonologic or only semantic codes. When Romani and Martin (1999) used such constraints, they found evidence of a common representational basis for short-term and long-term memory.

The Scoville and Milner (1957) and Prabhakaran et al. (2000) studies cited by **Patterson & Rypma** are readily reconciled with our framework. The Prabhakaran et al. results indicated that the right prefrontal cortex is involved in maintaining bindings in an active state. The Scoville and Milner findings indicated that the medial temporal lobe is crucial for consolidating bindings into long-term memory. These operations are not identical. Consolidation may be dependent upon maintaining bindings in an active state, but maintenance in an active state does not require consolidation operations. Thus, there is no reason to expect that identical combinations of brain sites are involved in the two operations. The **Ryan & Cohen** commentary provides a more incisive discussion of binding and memory (also see Grafman & Weingartner 1996).

The same reasoning applies to the Baddeley and Wilson (2002) study, cited by **Patterson & Rypma**. Consolidating new information requires binding of activated information to time and context, which amnesiacs can do, but this also requires additional processes that induce long-lasting changes in memory, at which amnesiacs are impaired. Note that in the questions raised by Patterson & Rypma, the central issue got reduced to differences in processing, not representational structure.

Accounting for phonologically based effects in the serial recall task poses no difficulties for a single representational basis. The phonological buffer is constituted by the activation of phonological codes contained in long-term memory (Martin et al. 1994). In the absence of evidence to the contrary, there is no need to assume that copies of representational contents are stored in a buffer that is distinct from long-term memory. The extent to which semantic codes contribute to the short-term memory process is determined by the nature of the task. Serial recall tasks emphasize phonology. Thus, lexical-semantic properties may contribute relatively little to recall of word order, although even in serial recall there can be some lexical-semantic contribution (Ruchkin et al. 1999). Semantic effects are more prominent in item recall, where word order is irrelevant (Cameron et al. 2004), or when meaning is emphasized, such as in semantic category cued-recall, in which case there may be no observable word-length effects (Haarmann & Usher 2001).

Patterson & Rypma claim that "the unitary-system account cannot easily explain observed capacity-limit differences that depend on the composition of to-be-remembered lists." Whether one accepts this conclusion depends upon what is meant by a unitary system. The target article's central, but limited, claim is that the representational basis of short-term memory is activated long-term memory. This view by no means excludes the existence of differentiable

memory processes. Patterson & Rypma claim that a unitary memory theory cannot account for findings such as that recall is better for sentences than for word lists, and that chunking in retrieval structures can overcome capacity limits in short-term memory performance. These findings seem to be neutral with respect to the central issue of the target article, namely, whether the contents of short-term memory are activated long-term memory or are stored in a separate buffer.

Even though activated long-term memory is the representational basis of short-term memory, distinctions can be made between long- and short-term memory processes. For example, the neural mechanisms involved in maintaining activation over time (a short-term memory process) may not be identical to the neural mechanisms involved in storage to and retrieval from long-term memory.

Vallar's commentary also draws upon neuropsychological studies to argue for separate short-term and long-term stores. Vallar claims that experiments with brain-injured patients typically provide evidence for the independence of discrete components, because "one single component may be selectively impaired, but the remaining parts of the system are still fully operative" (para. 2). We regard this claim as dubious. It is not likely that brain damage will be confined entirely to a single component of a system. Neuropsychological deficits are rarely pure, and double dissociations are often presented in terms of different patterns of relative deficits in two domains (R. Martin, personal communication).

This is the case for patient AB from the Romani and Martin (1999) study that **Vallar** uses to argue for distinct short-term and long-term stores. Patient AB displayed a severe semantic deficit in tests of both short- and long-term memory, and a mild phonological deficit. This was discussed by Martin et al. (1994), in which they pointed to a contrasting pattern of results for patient EA, who displayed a severe phonological deficit in short-term and long-term memory tests. Vallar tries to account for AB's memory problems in terms of a phonological deficit plus an impairment in lexical-semantic long-term memory, without explicitly acknowledging the existence of a lexical-semantic short-term retention process, which is clearly indicated by the available evidence (Haarmann & Usher 2001; Haarmann et al. 2003b; Hanten & Martin 2000; Martin & Romani 1994; Ruchkin et al. 1999). Vallar's argument confuses different types of representations with different types of memory systems (phonological for short-term, lexical-semantic for long-term) and is inconsistent with the Baddeley et al (1988) study cited in his commentary. That paper reported a patient (PV) with a short-term memory phonological deficit who also had a deficit in long-term learning of new phonology, thus implying a link between short-term storage and long-term learning.

Majerus et al. mistakenly took the results of the experiment presented in section 3.3 of the target article (the contrast of ERP activity during retention of words or pseudo-words) as the basis for our argument that short-term memory is activated long-term memory. The purpose of that experiment was to demonstrate that verbal short-term memory had a lexical-semantic component. The results did not bear upon the issue of short-term memory as activated long-term memory. The key experiment for the activated long-term memory issue was presented in section 3.6 (greater activation of "priming" words when they are ac-

tively maintained in short-term memory). The design of that experiment was such that its conclusion did not depend on ERP topography. Rather, the variation of ERP amplitude with experimental condition was the key dependent variable, and the results specifically indicated that representations in long-term memory were at a higher level of activation when active maintenance in short-term memory was required.

With regard to ruling out the possibility that, in addition to long-term memory stores, there are anatomically very close short-term memory buffers, it cannot be done at this time, if ever. As we remarked on the **Düzel** commentary, a null hypothesis cannot be proved. **Majerus et al.**'s suggestion of functionally distinct short-term memory buffers is not parsimonious and lacks clear supporting data. What would be the neural and cognitive architecture that distinguishes a buffer from adjacent cortex? One would expect dramatic dissociations between short- and long-term memory with lesions practically adjacent to each other in cortex. This has not been observed. With regard to Majerus et al.'s data from the three patients with short-term memory deficits, the results do not compel a separate short-term buffer interpretation. There may be enough intact cortex to activate long-term memory representations of lexical-semantic knowledge, but still be damage to connections between prefrontal and posterior cortex that are supposed to refresh the activations in long-term memory.

R7. Activated long-term memory and novelty

The **Kroger** and **Phillips** commentaries both remark on the perception, creation, and storage of novel information. We are all in agreement that such operations cannot simply be a matter of activation of long-term memories. However, we believe that it is incorrect to claim that novel contents may not depend on long-term memories. Consider Kroger's example of the proposition "John loves Mary" in a situation where one can distinguish it from "Mary loves John" (i.e., can infer who did what to whom) and one knows "nothing" about John (i.e., has never met John, does not know to whom the name John refers, and has never encountered the proper name John). It is clear that in such a situation various types of existing, activated long-term memories will nevertheless be associated with John. These may include: the phonology of the word John, the inference that John must be a proper name and has the syntactic category of noun, that John is probably human, that John can be an agent of the action love and grammatical subject of the verb love, that John and Mary co-exist and may have met, that John is part of an episodic context and time (e.g., hearing the sentence at a certain time with a certain linguistic and emotional prosodic stress), and so on (Haarmann, personal communication). Human thought simply cannot exist independent of already known memory elements, which is why analogies are so important to us (cf. Holyoak & Thagard 1997).

R8. Decay, displacement, and sleep

In discussing the issue of memory decay versus displacement in memory, the **Cowan** commentary mentioned a study of mildly cognitively impaired patients (Della Sala et

al., in press) who displayed better recall for a story after a one-hour delay when interference was minimized. It was noted that two of the patients slept during the retention interval, and therefore were not consciously rehearsing the story, yet they had better recall than when they were awake and exposed to interference. Cowan conjectures that there is a type of memory activation "that may preserve the most recent information for long periods." Another possible explanation is that this was an example of memory consolidation during sleep (Hobson & Pace-Schott 2002). There is considerable evidence that rapid-eye-movement sleep contributes to consolidation of procedural memories and some evidence that the early stage of non-rapid-eye-movement sleep contributes to consolidation of episodic memories. The duration of the delay-sleep interval could readily have allowed an early stage of non-rapid-eye-movement sleep that contributed to consolidation and, in turn, improved recall performance.

R9. Conclusion

Raaijmakers & Shiffrin state that "an approach that treats short-term memory as activated long-term memory is not inherently in conflict with information recycling in a limited-capacity . . . store" (Abstract). We do not disagree with this point. However, we do disagree with the position that whether one views short-term memory as activated long-term memory or separate stores is a theoretical question. We see it as an empirical question. Are there short-term stores at brain locations that are distinct from the long-term stores? This question can only be settled with hard data, not by appropriately formulating theoretical models. Without hard data, theoretical modeling is the equivalent of curve fitting, and that is at the root of the continuing controversies alluded to by Raaijmakers & Shiffrin.

In sum, we see no compelling reason, based on the commentaries we received, to adjust our thinking about the relationship between short-term and long-term memory. We claim that long-term memory structures can be distinguished based on category and domain of representation, and that the temporary activation of these representations is what is typically thought of as short-term memory in cognitive science. We would expect that a selective set of molecular and synaptic structures are recruited for an activated long-term memory representation (i.e., short-term memory) compared to its usual dormant state, but this biological differentiation does not imply a topography or psychological structure that is distinct from long-term memory. We argue that by ignoring differences in form of representation, many investigators have confused differences in representational form (e.g., object feature or orthographic envelope) with distinct memory systems, which has resulted in an explosion of memory systems and processes, which is, paradoxically, slowly beginning to resemble the domains of representation that we are arguing for in this target article. The importance of our arguments is reflected in the choice that an investigator must make in designing studies and conceptualizing how memory interacts with form of representation and in determining the roles of the various types of bindings in creating episodes. We think that an emphasis on deciphering the forms of representation is best done by the methodology of cognitive neuroscience and will result in a more rapid functional mapping of the cerebral cor-

tex and subcortical structures. Deciphering the molecular and synaptic codes allowing short-term activated states of long-term memory is in the realm of biology, and better suited for neurobiological methods.

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Letters “a” and “r” appearing before authors’ initials refer to target article and response, respectively.

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