

Psychological and Neural Mechanisms of Short-term Memory

Cindy A. Lustig
Richard L. Lewis
Marc G. Berman
Derek Evan Nee
Katherine Sledge Moore
John Jonides

University of Michigan

Address correspondence to:

Professor Cindy A. Lustig
Department of Psychology
University of Michigan
530 Church Street
Ann Arbor, MI 48109-4130

To comprehend this sentence, you must hold the beginning phrase in mind while reading and processing the rest of the words. The ability to remember and process information over a short time is essential to almost any activity, making short-term memory essential for cognition. In this chapter, we integrate psychological constructs of short-term memory that are drawn from behavioral data with their likely neural bases, especially as revealed by studies of patients and studies that use neuroimaging. Our discussion is organized around three questions that any account of short-term memory must address:

1. What is the structure of short-term memory?

A proper theory must describe an architecture that implements the short-term storage of representations. The dominant answer to this question has long been a model consisting of short-term storage buffers that are coordinated by a central executive and that are dissociable from long-term storage. Recently, there has been a shift toward models that do not distinguish short- and long-term stores. Instead, these models posit that short-term memory consists of a focus of attention that operates upon perceptual and long-term memory representations. Our review focuses on these latter models and their likely neural underpinnings.

2. What processes operate on the stored information?

A proper theory must articulate the processes that create and operate on representations, and how these processes can be implemented within the structure described above. These processes may include encoding and maintenance operations, shifts of the attentional focus, and retrieval of items into the focus of attention. Although rehearsal is often colloquially associated with short-term memory, we argue that it represents a strategic use of retrieval rather than a primary process.

3. What causes forgetting?

A complete theory of short-term memory must describe how information learned only seconds ago can be forgotten. We consider the behavioral and neurophysiological evidence for the two dominant accounts of forgetting, interference and decay, and we suggest a possible mechanism for short-term forgetting that may underlie both proposed accounts.

After addressing these questions, we sketch out a model that illustrates the links between psychological constructs and neural structures as an item moves through the stages of short-term memory from initial perception, maintenance over time and in the face of interfering information, and ultimate retrieval back into the focus of attention. To presage that model, we argue here that short-term memory exhibits the following properties:

1. Short-term memory consists of the temporary activation of long-term memory or perceptual representations
2. This temporary activation is severely limited to at most four representations
3. There are elementary processes that operate on these representations to encode, maintain, and retrieve them
4. Forgetting is largely accounted for by interference among competing representations.

Let us lay out our case.

1. The Structure of Short-Term Memory

1.1 The classic model: Short-term and long-term memory as separate stores

Any discussion of short-term memory must begin with the highly influential model developed by Baddeley and colleagues (e.g., 1986, 1992; Baddeley and Hitch, 1974; Repov and Baddeley, 2006). This model is the prototypical example of multi-store models of short-term memory. The defining feature of these models is that they describe short-term memory (STM) as a separate store from long-term memory (LTM). That is, information held in mind over the course of a few seconds is stored separately from information held over the course of long periods of time. Other common features include the separation of STM into different buffers based on information modality, and separation between storage buffers and the executive control processes that coordinate the buffers and operate on the material within them.

Figure 1 illustrates Baddeley's working memory model (Baddeley & Hitch, 1974; Baddeley, 2000) and the brain structures that have been linked to each component (Smith & Jonides, 1999). Fundamental components of the model include the short-term storage buffers, which are different for different types of information, and from long-term storage. The phonological loop is assumed to hold information that can be rehearsed verbally (e.g. letters, digits). A visuospatial sketchpad is assumed to maintain visual information and can be further fractionated into visual/object and spatial stores (Smith et al., 1995; Repov and Baddeley, 2006). An episodic buffer that draws on the other buffers and LTM has been added to account for the retention of multimodal information (Baddeley, 2000). A separate central executive is responsible for working memory processes that require operations on the items stored in the buffers. This central executive is also thought to be responsible for coordinating the interplay among the various buffers and their interactions with LTM.

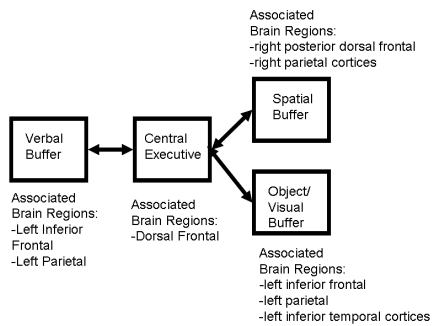


Figure 1: Baddeley's Working Memory Model

The earliest evidence for separate buffers by modality came from studies showing that secondary verbal tasks interfered with verbal STM but not visual STM, and vice versa (e.g., Brooks, 1968; Den Heyer & Barrett, 1971). This double dissociation implied uniquely verbal processes for verbal STM, and uniquely visual processes for visual STM, arguing for separate stores. More recent neuroimaging research has further investigated the neural correlates of the reputed independence of STM buffers. Verbal STM has been shown to rely primarily on left inferior frontal and left parietal cortices, spatial STM on right posterior dorsal frontal and right parietal cortices, and object/visual STM on left inferior frontal, left parietal, and left inferior temporal cortices (e.g., Jonides et al., 1993; Awh et al., 1996; Smith and Jonides, 1997; see review by Wager & Smith, 2003). Verbal STM shows a marked left-hemisphere preference, whereas spatial and object STM can be distinguished mainly by a dorsal versus ventral separation in posterior cortices (consistent with Ungerleider and Haxby, 1994; see Baddeley, 2003, for an account of the function of these regions in the service of STM). These neural dissociations provide further evidence for separable short-term stores.

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The idea of separate storage by modality is still well-accepted, especially with regard to the posterior regions (e.g., left parietal for verbal, right parietal for spatial). However, the rest of Baddeley's model – which argues for separable STM and LTM systems – is less well-supported.

Initially, the most compelling data to motivate a separation of STM from LTM came from brain-injured patients who seemed to show a double dissociation between the two systems. Patients with parietal and temporal lobe damage showed impaired short-term phonological capabilities but intact long-term memory (Shallice & Warrington, 1970; Vallar & Papagno, 2002). Conversely, patients with medial temporal lobe (MTL) damage were often claimed to demonstrate impaired long-term memory but preserved short-term memory (e.g., Baddeley & Warrington, 1970; Scoville and Milner, 1957). However, some recent papers suggest that MTL patients' real problem may be forming new associations and bindings, a process preferentially tapped by long-term episodic memory tests, but that can also be endemic in STM tests. For example, if the task requires associating an item with a

particular spatial location, these patients show profound deficits even after very short delays (Olson et al, 2006). On the other side of the STM/LTM dissociation, patients with left perisylvian damage that results in STM deficits also have deficits in phonological processing in general, suggesting a deficit that extends beyond STM per se (e.g., Martin, 1993). Finally, functional neuroimaging data from healthy adults also suggest that STM and LTM have more commonalities than differences (e.g. Braver et al., 2001; Cabeza et al., 2002; Ranganath & Blumenfeld, 2005). Thus, the view that STM and LTM are separable based on studies of patients is open to reinterpretation.

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Another argument for separate STM and LTM systems comes from the assumption that the two types of memory are stored in separate areas of the brain; however, this assumption may be false. Early work showed single-unit activity in dorsolateral prefrontal cortical regions (principal sulcus, inferior convexity) that was selectively responsive to memoranda during the delay (retention interval) of STM tasks. This delay activity was interpreted as evidence that these regions were the storage sites for STM (e.g., Fuster, 1973; Funahashi et al., 1989; Wilson et al., 1993; see Jacobsen, 1936 for preceding lesion work). However, the sustained activation of frontal cortex during the delay period does not necessarily mean that this region is a site of STM storage. Many other regions of neocortex also show activation that outlasts the physical presence of a stimulus and provides a possible neural basis for STM storage.

The alternative view that we promote is that prefrontal cortical involvement in STM reflects the operation of processes that guide the use (encoding, maintenance, and retrieval) of information that is primarily perceived and stored via posterior regions (the same areas of purported LTM storage). This view receives support from studies showing that prefrontal cortical involvement may not be necessary for STM except in the face of distraction (Malmö, 1942, Postle and D'Esposito, 1999). By contrast, patients with left temporo-parietal damage show deficits in phonological storage, regardless of the effects of interference (Vallar & Baddeley, 1984; Vallar & Papagno, 2002).

One item on which multi-store and unitary-store models agree is that central executive control processes are primarily implemented by prefrontal cortex. A meta-analysis of 60 functional neuroimaging studies indicated that increased demand for executive processing recruits dorsolateral frontal cortex and posterior parietal cortex (Wager & Smith, 2003). By contrast, storage processes recruit predominately posterior areas in primary and secondary association cortex. These results corroborate the evidence from lesion studies and support the distinction between storage and executive processing.

1.2 Unitary-store models: STM as the focus of attention

Figure 2 illustrates several unitary-store models. The shared assumption of these models is that STM consists of a temporary activation of the same representations used for initial perception and LTM. As shown in the figure, the types of activation associated with STM may include both a privileged status in the focus of attention (most likely implemented by active firing of the neurons involved in the representation) and out-of-focus but highly-activated representations within LTM (perhaps represented by short-term plasticity and synchronization of spontaneous activity in the neurons composing the representation). As we elaborate below, the major distinction among models within the unitary-store family concerns the size or capacity of the attentional focus.

Early versions of unitary-store models (e.g., Anderson, 1983; Atkinson & Shiffrin, 1971; Hebb, 1949) fell out of favor during the predominance of the multi-store account. As described above, recent developments have called some of the assumptions of the multi-store model into doubt (see Jonides et al. (in press) and Postle (2006) for a more detailed discussion of the issues). At the same time, unitary-store models have been revived and elaborated by Cowan (1988, 1995, 1999, 2000), McElree (2001), Oberauer (2002), Verhaegen et al. (2004), Anderson et al. (2005) and others.

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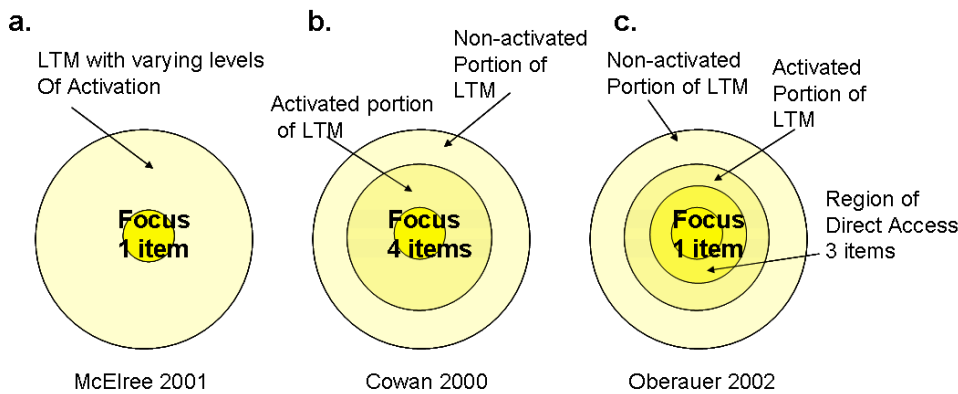


Figure 2: Unitary STM models

Importantly, the idea of “unitary stores” used in this context is not the same as a “unitary memory” idea. The unitary stores concept acknowledges the functional specialization of brain regions and processes (e.g., consolidation), and that the degree to which different memory systems are involved in the processing of an item is highly correlated with (though not completely determined by) the passage of time. We expand on this idea in section 4, where we sketch out a model of STM, but at least some

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discussion of the idea of how representations are shared among perception, STM, and LTM may be useful here. (See Oberauer, 2002 for a similar discussion.)

When an item is initially perceived, it activates a distributed set of neurons throughout the brain regions involved in processing its different feature components: For a visually-presented item, these would include some neurons in V4 that code color information about the object, some in inferotemporal cortex that code shape information, and so on. Medial temporal lobe structures are involved in processing contextual information, including those aspects later needed for episodic memory. Depending on consolidation processes, the coordinated pattern of activation among the different feature components ultimately results in synaptic changes and long-term storage.

Where does STM fit into this picture? Our take on this question is most like Oberauer's (2002; see panel C of our Figure 2). One representation is in the focus of attention, either as the result of recent perception or retrieval from LTM. The network of neurons involved in this representation is likely actively firing in conjunction with frontal and parietal networks involved in attention to that representation. This representation is immediately available and accessible. A limited set of other recently perceived/retrieved representations are not in the focus, but maintain a relatively high level of activation and availability, perhaps implemented by short-term plasticity mechanisms such as increased coordination of spontaneous activity (Destexhe & Contreras, 2006; Sussillo et al., 2007). This is the region that Oberauer (2002) terms the region of direct access, where roughly 3 items are in a heightened state of activation and can be accessed faster than those in the activated portions of LTM, but slower than those in the focus of attention.

In short, unitary-store models posit that perception, STM, and LTM use the same underlying representations, but the state of those representations (active firing, short-term plasticity, long-term plasticity) may differ depending on which of these functions is involved. This contrasts with multi-store models, which posit STM buffers that are separate from LTM storage. Unitary- and multi-store models agree that posterior regions are clearly differentiated by information type (e.g., auditory, visual, spatial). However, they differ in their view of frontal activations: Unitary-store models view these as primarily related to processes operating upon the representations, especially those involved in selecting a representation for the focus of attention and keeping it there. From the multi-store perspective, frontal activations are related to the representational buffer per se. Our view favors the unitary-store models, which receive significant support from neuroimaging studies, lesion data, and modeling work (see reviews by Damasio, 1989; McClelland et al., 1995; Reuter-Lorenz & Jonides, 2007).

1.3 Controversies over capacity

Regardless of whether one subscribes to multi- or unitary-store models, an important question is how much information can be held within a storage buffer (multi-store models) or the focus of attention (unitary-store models). Multi-store models describe capacity limits as dependent on the individual buffers, in particular the speed

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with which information can be rehearsed in that buffer versus the speed with which information is forgotten (Baddeley, 1986, 1992; Repov and Baddeley, 2006). In the verbal domain, for example, it has been shown that approximately two-seconds worth of verbal information can be re-circulated successfully (e.g., Baddeley et al 1975).

In unitary-store models, there may be some constraints imposed by the material-specific aspects of the representation, but the critical questions surround the capacity of the focus of attention. Even Miller's classic (1956) paper acknowledged that the traditional estimate of "seven plus or minus two" is too large because it is based on studies that allowed participants to engage in processes of rehearsal and chunking, and therefore reflects contributions of the focus of attention, selectively activated representations, and LTM (see also Cowan, 2000; Waugh & Norman, 1965.) Current models differ on whether the capacity is four items (Cowan, 2000) or only one (McElree, 2001; Garavan, 1998; Verhaeghen & Basak, in press). Figure 2 shows the slight variations among these unitary STM models. Since we generally favor the unitary-store models, we limit our discussion of capacity limits to their debate.

1.3.1 Behavioral and neural evidence for the magic number 4.

Cowan (2000) has reviewed an impressive array of studies leading to his conclusion that the capacity limit is four items, plus or minus one (e.g., Sperling, 1960; see Cowan's Table 1). An important line of evidence comes from change-detection and other tasks that do not require the serial recall of individual items which may lead to interference in output and therefore underestimate capacity. For example, Luck and Vogel (1997) presented subjects with 1 to 12 colored squares in an array. After a blank interval, another array of squares was presented, in which one square may have changed color. Subjects were to respond whether the arrays were identical. In these experiments and others (e.g, Pashler, 1988), there are sharp drop-offs in performance after approximately four items.

Electrophysiological and neuroimaging studies also support the idea of a 4-item capacity limit. The first such report was by Vogel and Machizawa (2004) who recorded event-related potentials (ERPs) from subjects as they performed a visual change-detection task. ERPs recorded shortly after the onset of the retention interval in this task indicated a negative-going wave over parietal and occipital sites that persisted for the duration of the retention interval and was sensitive to the number of items held in memory. Importantly, this signal plateaued when the array size reached between three and four items. The amplitude of this activity was strongly correlated with estimates of each subject's memory capacity and was less pronounced on incorrect than correct trials, indicating that it was strongly related to performance. Subsequent fMRI studies have observed similar load- and accuracy-dependent activations, especially in intraparietal and intraoccipital sulci (Todd & Marois, 2004, 2005). These particular regions have been implicated by others (e.g., Yantis and Serences, 2003) in the control of attentional allocation, supporting the idea that one rate-limiting step in STM capacity has to do with the allocation of attention (Cowan, 2000; McElree, 1998, 2001; Oberauer, 2002).

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1.3.2 Evidence for more severe limits on focus capacity.

Others argue for a much more limited capacity of just one item (e.g., McElree, 2001; Garavan, 1998, Verhaeghen & Basak, in press). This estimate is based on studies using a combination of response time and accuracy as measures of performance. For example, Garavan (1998) required subjects to keep two running counts in STM, one for triangles and one for squares—as shape stimuli appeared one after another in random order. This task can be seen in Figure 3.

Subjects controlled their own presentation rate, and Garavan measured the time spent processing each figure before moving on to the next. Responses to a figure of one category (e.g., a triangle) that followed a figure from the other category (e.g., a square) were fully 500 ms longer than responses to the second of two figures from the same category (e.g., a triangle followed by another triangle). These findings suggested that attention could be focused on only one internal counter in STM at a time. Switching attention from one counter to another incurred a substantial cost in time.

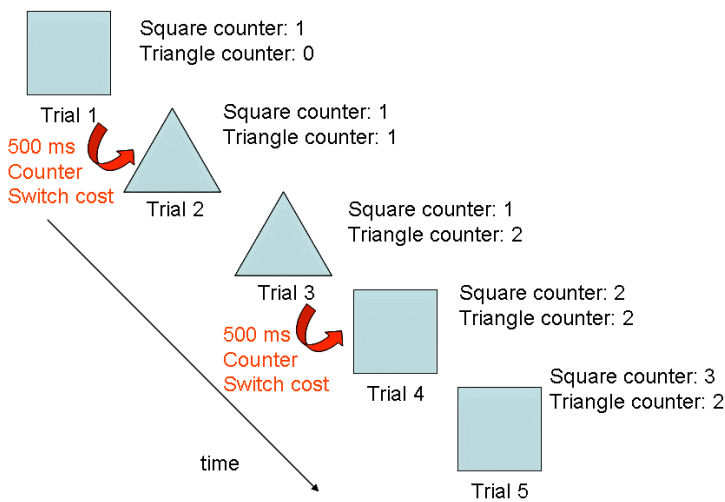


Figure 3: The Garavan counter updating task

Other evidence comes from McElree (1998) who found that the last item in a list was retrieved substantially faster than other items, suggesting that it was still in the focus. Other items were retrieved at a rate that was substantially slower than the last item. Those other items, however, were retrieved at similar rates (which McElree deems a measure of *accessibility*), despite differing in accuracy (which McElree describes as a *measure of availability*).

Oberauer (2002) suggested a compromise solution to the “one versus four” debate. In his model, up to four items can be *highly* accessible, but only one of these items can be

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in the focus of attention. This model is similar to that of Cowan (2000), but adds the assumption that an important method of accessing short-term memories is to focus attention on one item, depending on task demands. Thus, in tasks that serially demand attention to several items (such as those of Garavan, 1998, or McElree, 2001) the mechanism that accomplishes this involves changes in the focus of attention among temporarily activated representations in LTM.

1.3.3 Alternatives to capacity limits based on number of items.

Some researchers disagree with fixed item-based limits, in part because these limits seem mutable. For example, practice may improve subjects' ability to use processes such as chunking to allow greater capacities by tying together individual items into a single unit (McElree 1998; Verhaeghen et al., 2004, but see Oberauer, 2006). However, proponents of the fixed-capacity view might retort that practice alters the amount of information that can be compacted into a single representation, not the total number of representations that can be held in STM (Miller, 1956).

Another attack on fixed-capacity views comes from questioning the assumption that items are the appropriate unit for expressing capacity limits. Wilken and Ma (2004) demonstrated that a signal-detection account of STM, in which STM capacity is primarily constrained by noise, better fit behavioral data than an item-based fixed capacity model. Recent data from change-detection tasks suggest that object complexity (Eng et al, 2005) and similarity (Awh et al, 2007) play an important role in determining capacity. Xu and Chun (2006) offer neuroimaging evidence that may reconcile the item-based and complexity accounts: in a change-detection task, they found that activation of inferior IPS tracked a capacity limit of four, but nearby regions were sensitive to the complexity of the memoranda, as were the behavioral results.

Building on these findings, we suggest a new view of capacity. The fundamental idea that attention can be allocated to one piece of information in memory is correct, but the definition of what that one piece is needs to be clarified. It cannot be that just one item is in the focus of attention at any one time, because if that were so, hardly any computation would be possible. How could one add $3+4$, for example, if attention could be allocated only to the "3" or the "4" or the "+" operation? We propose that what attention focuses on is what is bound together into a single functional context, whether that context is defined by time, space, or some other stimulus characteristic such as similarity or task relevance. By this account, attention can be placed on the whole problem " $3+4$ ", allowing relevant computations to be made.

Put another way, the critical unit is at the level of representation as perceived by the subject. This is not necessarily the same as the physical "item" presented by an experimenter. Chunking is one special case of a single representation holding multiple items. One can also think of more everyday examples: In considering this chapter, the level of representation could be the entire chapter, the current page, a single word, or a single letter. Letters are bound together by the functional context of a word, and so on. Complexity comes into play by limiting the number of subcomponents that can be bound

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into one functional context. This approach has the advantage of permitting novel relations to be established among familiar items, by allowing novel combinations of individual components and contexts to form new representations. This addresses one of the criticisms of the purest form of the unitary models: if STM is strictly limited to an activated portion of LTM, then the system can never entertain new thoughts.

1.4 Summary

What is the structure of STM? We favor the unitary-store model, in which the representational bases for perception, STM, and LTM are identical. That is, we argue that the same neocortical representations that are the repository of semantic knowledge are activated when a piece of information is maintained for the short-term, whether that activation is due to perceiving that information or retrieving it from LTM (Wheeler et al., 2004). Different regions of neocortex represent different types of information (e.g., verbal, spatial), and it is therefore to be expected that STM is also organized by information-type.

Empirically, STM often cashes out as the four or so items whose representations can be temporarily activated and processed simultaneously. However, this item-based limit is flexible and dependent on factors such as complexity and experience. The critical feature of unitary-store models is the severely limited focus of attention. While the capacity of that focus is still under debate, we believe it is one representation, although this representation may consist of several items bound together into one functional context. Of interest, for the relatively simple stimuli used in laboratory experiments, this limit also appears to be around four items, suggesting that it may be related to the factors that place a similar ~4 item limit on subitizing, another attention-demanding process.

2. The three core processes of STM: Encoding, maintenance, and retrieval

How does this structure work – that is, what are the processes of STM? Many have been suggested, including rehearsal, attention shifts, updating, and interference resolution. However, we argue that these complex processes represent combinations or special cases of three basic types, which govern the transition of memory representations into and out of the focus of attention: *Encoding* processes select sensory information and transform it into the representation that occupies the focus, *maintenance* processes keep the representation in the focus and protect it from interference or decay, and *retrieval* processes bring information from the past back into the focus.

2.1 Encoding items into the focus. Although detailed accounts of encoding processes are usually left to theories of perception, most accounts of STM make several assumptions about how encoding occurs.

First, perceptual information is assumed to have immediate but capacity-limited access to the focus of attention. Perceptual information can serve as the object of the focus

just as information from the past does. Several of the experiments cited by Cowan (2000) as evidence for a capacity of four involved representations of objects presented currently or less than a second ago. These include visual tracking experiments (Pylyshyn et al, 1994), enumeration (Trick & Pylyshyn, 1993), and whole-report of spatial arrays and spatiotemporal arrays (Sperling, 1960; Darwin et al, 1972). Similarly, in McElree's (2006) and Garavan's (1998) experiments, each incoming item in the stream of material (words or letters or objects) is assumed to be momentarily represented in the focus.

Second, current theories assume that encoding new representations into the focus results in the displacement of other representations. For example, in McElree's single-item focus model, each incoming item has its turn in the focus and replaces the previous item. The work reviewed above showing performance discontinuities after the putative limit of STM capacity has been reached appears to support the idea of whole-item displacement (e.g., Cowan, 2000; Garavan, 1998; McElree, 2001; Oberauer, 2002). On the other hand, it is not clear how simple item-based displacement accounts for the effects of similarity or complexity on capacity estimates. One possibility is that these factors influence how items compete with each other for access to the focus. Another possibility is that complexity and similarity influence the set of featural components needed to represent an item, and items compete with each other for this limited feature-based representational resource. In other words, the more overlap there is between the patterns of activation that represent two items (in V4, inferotemporal cortex, fusiform gyrus, etc), the more likely those items are to interfere with each other. We expand further on these ideas in the section 3, on forgetting.

Third, all current accounts assume that perceptual information does not have automatic, obligatory access to the focused state. Instead, given the severe limits on capacity, attentional control is required to ensure that task-relevant items are included in the focus, and task-irrelevant items are excluded. Postle (2005) recently found that while subjects maintained information in STM, increased activity in dorsolateral prefrontal cortex during the presentation of distracting material was accompanied by a selective decrease in inferior temporal regions involved in object representation. This pattern suggests that prefrontal regions selectively modulated posterior perceptual areas to prevent incoming sensory input from disrupting the representation of task-relevant memorandum.

Just as Postle (2005) found evidence to suggest that prefrontal activations prevent distracting sensory information from being encoded, we suggest that frontal and parietal areas are responsible for selective attention towards relevant inputs. This involves biasing posterior sensory regions towards important target stimuli. As these items are encoded, the medial temporal lobe binds each item to a functional context (e.g., a temporal and/or spatial context). Simultaneously, very short-term synaptic plasticity across cortical areas begin to encode the item's features and its bound context. Zucker & Regehr (2002) identify at least three distinct plasticity mechanisms which begin to operate on this time scale (tens of milliseconds), and which together are sufficient to

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produce memories lasting several seconds. (For the use of this mechanism in a prominent neural network model of STM, see Burgess & Hitch, 1999, 2005, 2006).

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2.2 Maintaining items in the focus. Once an item is in the focus of attention, what keeps it there? If the item is in the perceptual present, the answer is clear: attention-modulated, perceptual encoding. The more pressing question is: What keeps something in the cognitive focus when it is not currently perceived? For many neuroscientists, this is the central question of STM—how information is held in mind for the purpose of future action after the perceptual input is gone.

Extensive evidence from both humans and nonhuman primates supports the idea that prefrontal-posterior circuits underlie active maintenance. The role of posterior perceptual regions is relatively clear; activity in these regions likely recapitulates the initial perceptual encoding of the representation, but what of the activation in prefrontal circuits? For example, there is classic evidence from single-cell recordings showing that some neurons fire selectively during the delay period in delayed-match-to-sample tasks (e.g., Fuster, 1973; Funahashi, et al., 1989). Does this activation (and its counterpart in human neuroimaging studies, e.g., Jha & McCarthy, 2000) suggest that a representation of the information is also held in the prefrontal cortex, or does it reflect some other process?

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As mentioned above, early interpretations of these frontal activations linked them directly to STM representations (Goldman-Rakic, 1987). By contrast, more recent theories suggest they subserve attentional control processes that maintain representations in posterior areas (Raganath, 2006, Ruchkin, Graman, Cameron & Berndt, 2003; Pasternak & Grenlee, 2006). For example, maintenance operations may modulate perceptual encoding to prevent incoming perceptual stimuli from disrupting the focused representation in posterior cortex (Postle, 2005). Mechanistic descriptions of how maintenance might occur are found in computational neural-network models hypothesizing that prefrontal cortical circuits support attractors, which are self-sustaining activation patterns observed in certain classes of recurrent networks (Hopfield, 1982; O'Reilly, 2005; Polk, Simen & Lewis, 2002). A major challenge is to develop computational models that are able to engage in active maintenance of representations in posterior cortex while simultaneously processing, to some degree, incoming perceptual material (see Renart (1999) for one example).

We prefer the following view of maintenance operations: prefrontal and parietal regions perform attentional control processes by signaling posterior sensory regions to continue a high level of activation for the representation that is currently in the focus of attention even after it is no longer physically presented. These control regions likely differ by type of material (e.g. Smith and Jonides, 1997). The attentional focus on this representation protects it from interference and decay and keeps it in an immediately accessible state. Other representations that are maintained in STM, but not in the focus, are supported by short-term plasticity mechanisms that increase the coordination or connection weights between the features of these representations. Stochastic variability in the neurons that make up these representations may eventually lead them to decay, and

they are also vulnerable to competitive interference from each other, other items in memory, or incoming stimuli. (Zucker & Regehr, 2002).

2.3 Retrieving items into the focus. Most major STM theories do not include detailed treatments of retrieval, although the limited-focus models assume that there is some way of bringing information from LTM into the focus. This process can be labeled “retrieval” (c.f. McElree, 2006; Sternberg, 1966), but that label does not imply the spatial metaphor of moving items from one store to another. Instead, it is important to keep in mind our assumption that the same underlying neural representations subserve both STM and LTM, and that the question is whether or not that representation is currently in the highly activated state that constitutes the focus.

There is now considerable evidence, mostly from mathematical models of behavioral data, that STM retrieval of item-information is a rapid, parallel, content-addressable process. Early models of STM retrieval (e.g., Sternberg, 1966) postulated a serial search process. However, current models favor a parallel search process because they can better account for reaction time data such as those shown in Figure 4. McElree and Doshier (1989) manipulated the response deadline in a standard item-recognition task, in which participants are presented with a rapid sequence of to-be-remembered verbal items (e.g., letters or digits), followed by a probe item. The task was to identify whether the probe was a member of the memory set. The speed at which an item was retrieved was thought to measure its accessibility (exhibited in Figure 4 by the rise to asymptote), whereas accuracy measured availability (exhibited in Figure 4 by the asymptote). As described previously, the last item (which is the most recent) is accessed more quickly than the others, suggesting that it is already in the focus. The other items are accessed at a uniform rate, suggesting a parallel search among them to bring them into the focus (see also Hockley, 1984; see review by McElree, 2006).

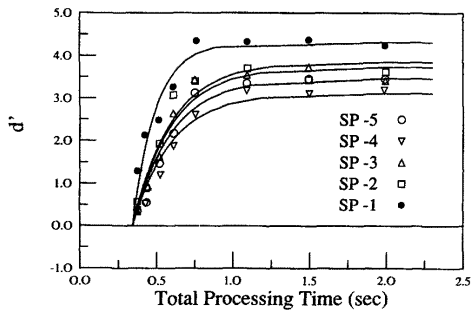


Figure 7. Observed average d' values as a function of total processing time for serial positions with set sizes three (SS3; top panel) and five (SS5; bottom panel). (Smooth functions are derived from the estimated parameters of the exponential model fits presented Table 3.)

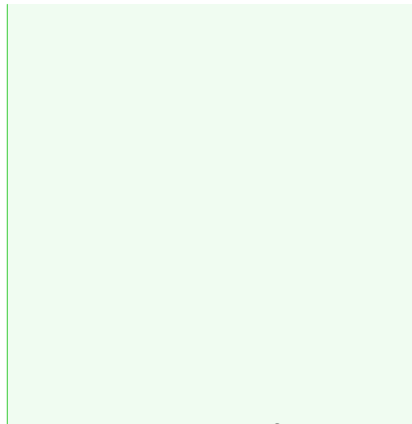


Figure 4: Results taken from McElree

and Doshier, 1989

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What are the neural underpinnings of STM retrieval, and does it differ—if at all—from LTM retrieval? As described earlier, similar activations in posterior perceptual regions support the idea that STM and LTM both operate on the same neural representations – that is, that they are similar in *structure* with regard to how representations are stored. STM and LTM may also be similar in *process*, at least when it comes to retrieval: The retrieval processes described above for STM are isomorphic with those posited for LTM (e.g. Anderson et al 2005; Gillund & Shiffrin, 1984; Murdock, 1982; Plaut 1997). Of course, this isomorphism logically follows from the idea that out-of-focus STM representations are simply LTM representations in a special state of activation, which may include short-term plasticity. This unification is one of the principal theoretical virtues of the recent STM retrieval models such as those championed by McElree (2006).

Extensive studies have delineated a network of medial temporal lobe (MTL) regions, lateral prefrontal regions, and anterior prefrontal regions active in long-term retrieval tasks (e.g., Buckner et al, 1998; Cabeza & Nyberg, 2000; Fletcher & Henson, 2001). As described earlier (see section 1.1), although MTL structures were originally thought not to play a role in STM, recent work has shown that they come into play when the task demands remembering novel information or making associations, regardless of the time scale.

Like the MTL, the frontal cortex is used similarly in retrieval for STM and LTM, as evidenced in numerous neuroimaging studies. For example, event-related studies of a standard STM probe-recognition task find activations in lateral prefrontal regions (e.g, D'Esposito, Postle, Jonides & Smith 1999; Monoach, et al, 2003; D'Esposito, 2000) and anterior prefrontal regions (Badre & Wagner, 2005) often implicated in LTM retrieval. Some of these studies used retention intervals that were somewhat longer than the typical behavioral STM task, making them vulnerable to the criticism that the activations in fact represented LTM retrieval. However, a meta-analysis of studies that involved bringing very recently-presented items into the focus of attention likewise found specific involvement of lateral and anterior prefrontal cortex (Johnson et al, 2005). Therefore, these regions appear to be involved in retrieval, regardless of time-scale.

Even stronger evidence derives from recent imaging studies that directly compare short-versus long-term retrieval tasks using within-subjects designs. The two types of tasks activate highly overlapping regions in dorsolateral, ventrolateral, and anterior prefrontal cortex (Cabeza, Dolcos, Graham & Nyberg, 2002; Ranganath, Johnson, D'Esposito, 2003; Talmi, et al., 2005). In some cases, STM and LTM tasks involve the same regions but differ in the relative amount of activation shown within these regions. For example, Cabeza et al. (2002) reported similar engagement of medial temporal regions in both types of task, but greater anterior and ventrolateral activation in the long-term episodic tasks. However, Talmi et al. (2005) reported greater activation in both medial temporal and lateral frontal cortices for recognition probes of the earliest items in a 12-item list (where LTM would be more prominent) versus the last or second-to-last items, (where STM would be more prominent). This discrepancy might be explained if items at the end of the list were still in the focus of attention, and thus did not require cue-based

retrieval processes. Notably, the end-of-list items preceded the probe by less than 2 seconds, within the time span classically suggested for verbal STM (e.g., Baddeley et al., 1975).

In summary, the bulk of the neuroimaging evidence points to the conclusion that the recruitment of frontal and medial temporal regions depends on whether the information is currently in or out of focus, not whether the task nominally tests short or long time spans (see Sakai, 2003 for a more extensive review). because these regions are not involved in memory storage per se. Thus, MTL regions will increase activation in response to items in a typical LTM or STM task if these items have fallen out of the focus of attention in order to retrieve their functional context. Likewise, frontal regions will increase activation when any item (from an LTM or STM task) is being retrieved into the focus of attention during rehearsal or in preparation to make a response. Frontal regions are thought to perform several operations during retrieval including initiating retrieval, accessing stored representations, and selecting amongst competing representations (Sakai, 2003; Badre and Wagner, 2007).

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2.4 The relationship of STM processes to rehearsal

Rehearsal intuitively seems like the prototypical STM process. However, many formal and computational theories of STM exclude rehearsal from their list of core processes (e.g., Anderson & Matessa, 2002; Burgess & Hitch, 2006; Kieras et al., 1999). For example, Cowan (1999, 2000) provides evidence that first-grade children do not use verbal rehearsal strategies, but nevertheless have measurable STM capacities. In fact, Cowan (2000) uses young children's failure to use rehearsal to argue that their performance is indicative of the fundamental capacity limits of STM.

We take the view that rehearsal is simply a controlled sequence of retrievals and re-encodings of items into the focus of attention (c.f., Baddeley, 1986; Cowan 1995). The theoretical force of this idea becomes apparent when it is coupled with our other assumptions about the structures and processes of the underlying STM architecture. We briefly sketch here two interesting sets of empirical predictions that follow from this view.

When coupled with the idea of a single-item focus, the assumption that rehearsal is a sequence of retrievals into that focus makes a clear prediction: A just-rehearsed item should display the same retrieval dynamics as a just-perceived item. This prediction was directly tested by McElree (2006) using a version of his response-deadline recognition task. A retention interval occurred between the list-presentation and the probe, and subjects were trained to rehearse the list at a particular rate during that interval. Knowing the rate at which subjects rehearsed made it possible to know when each item was rehearsed, and thus when it was hypothetically re-established in the focus. The results were compelling: A just-rehearsed item showed the same fast retrieval dynamics that typify a just-perceived item in experiments without a retention interval (see section 2.3). In other words, the difference in speed-accuracy tradeoff functions for in-focus versus out-of-focus items was apparent regardless of whether the

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dichotomy was established by internally-controlled rehearsal or externally-controlled perception.

The assumption that rehearsal is a controlled strategy also yields interesting predictions. If rehearsal is the controlled composition of more primitive STM processes, then rehearsal should activate the same brain circuits as the primitive processes, along with additional (frontal) circuits associated with their control. In other words, there should be overlap of rehearsal with brain areas subserving retrieval and initial perceptual encoding. Likewise, there should be control-areas distinct from those of the primitive processes.

Both predictions receive support from neuroimaging studies. The first prediction is broadly confirmed: There is now considerable evidence for the re-activation of areas associated with initial perceptual encoding in tasks that require rehearsal (see Jonides, Lacey & Nee, 2005, for a recent review; note also that there is evidence for reactivation in LTM retrieval: Wheeler, 2000; 2006). The second prediction—that rehearsal engages additional control areas beyond those participating in maintenance, encoding, and retrieval—receives support from two effects. One is that verbal rehearsal engages a set of frontal structures associated with articulation and its planning: supplementary motor, premotor, inferior frontal, and posterior parietal areas (e.g., Jonides et al, 1998; Smith & Jonides, 1999; Chein & Feiz, 2001). The other is that spatial rehearsal engages attentionally-mediated occipital regions, suggesting rehearsal processes that include retrieval of spatial information (Awh et al. (1998, 1999, 2001).

In summary, there is substantial evidence supporting the idea that rehearsal is a process composed of more fundamental STM processes, namely retrieval and encoding. In addition, a just-perceived item is functionally equivalent to a just-rehearsed item, showing that the focus of attention has similar properties in these two cases.

3. Why do we forget?

Forgetting in STM is a vexing problem: What accounts for failures to retrieve something encoded just seconds ago? There are two major explanations for forgetting, often placed in opposition: time-based decay and similarity-based interference. Below, we describe some of the major findings in the literature related to each of these explanations, and we suggest that they may ultimately result from the same underlying principles.

3.1 Decay theories: Intuitive but problematic

The central claim of decay theory is that as time passes, information in memory erodes, and so it is less available for later retrieval. This explanation has strong intuitive appeal. However, theories of STM that rely on decay to explain forgetting face two strong criticisms. First, experiments attempting to demonstrate decay can seldom eliminate confounds and alternative explanations. Second, most psychological theories that posit

decay do not include a mechanistic explanation of how it might occur. Without such an explanation, it is difficult to see decay theories as any more than a restatement of the phenomenon. Below we review the debates on this issue and ultimately suggest a possible mechanism for decay.

3.1.1 Retention-interval confounds: Controlling for rehearsal and interference.

The classic Brown-Peterson procedure (Brown, 1958, Peterson & Peterson, 1959) illustrates many of the difficulties in providing evidence for decay. In this procedure, participants were asked to learn consonant trigrams (e.g., DPW). Each trigram was followed by a retention interval during which participants counted backwards to prevent rehearsal, followed by their attempt to recall the trigram. Performance decreased as retention interval increased, apparently providing good evidence for time-based decay. However, Keppel and Underwood (1962) showed that almost no forgetting occurs for the earliest trials, regardless of the retention interval. The effects of the retention interval became apparent only after several trials had passed, suggesting that proactive interference from previous memoranda was the major mechanism of forgetting, and that it was this influence that increased over time.

A major problem in testing decay theories is controlling for what occurs during the retention interval, especially with human subjects. One common method is to attempt to prevent rehearsal by requiring subjects to perform another attention-demanding task during the interval - for example, the requirement to count backwards during the Brown-Petersen task. However, the difficulty of the retention-interval task does not appear to influence the amount of forgetting that occurs, raising the possibility that the retention-interval task relies on a different resource-pool than does the primary memory task, and thus may not ultimately be effective in preventing rehearsal (Roediger, Knight, & Kantowitz, 1977).

Another problem is that most tasks that fill the retention interval require subjects to use STM. This could lead to active displacement of items from the focus of attention (e.g., McElree, 2001). Thus, the problem with retention-interval tasks is that they are questionable in preventing rehearsal of the to-be-remembered information, and they also introduce new, distracting information that may engage STM.

Several attempts have been made to escape the rehearsal conundrum by using stimuli that are not easily converted to verbal codes (e.g., pure tones; Harris, 1952) or by varying the retention interval during *implicit* memory procedures, where participants do not know that their memory is being tested, and so they would have no reason to rehearse (McKone, 1995). These experiments provide some of the best behavioral evidence for decay, although they are still somewhat vulnerable to Keppel and Underwood's (1962) criticism about prior trials.

Another potential problem is that even if they are not deliberately rehearsing, participants' brains and minds are not inactive during the retention interval (Raichle, 2001). There is increasing evidence that the processes ongoing during nominal "resting states" are related to memory, including STM (Hampson et al., 2006). Spontaneous

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retrieval of other memories during the retention interval could interfere with memory for the experimental items. So, although experiments that reduce the influence of rehearsal provide some of the best evidence of decay, they are not definitive.

3.1.2 What happens neurally during the delay? Stimulus-associated neural activity usually declines during a retention interval. This decline seems like a prime candidate for a mechanism of decay. However, it has been more difficult than expected to show a relation between reduced neural activity and reduced memory.

Single-cell results like those of Fuster (1995) are often cited as evidence for decay. In monkeys performing a delayed-response task, delay-period activity in inferotemporal cortex steadily declined over 18 seconds (see also Pasternak, 2005). At a molar level, human neuroimaging studies often show delay-period activity in prefrontal and posterior regions, and this activity is often thought to support maintenance or storage (see review by Smith & Jonides, 1999). As reviewed above, it is likely that the posterior regions support storage, and that frontal regions support processes related to interference-resolution, control, attention, response preparation, motivation and reward.

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Consistent with the primate data, Jha & McCarthy (2000) found a general decline in activation in posterior regions over a delay period, which suggests some neural evidence for decay. However, this decline in activation was not obviously related to performance, which suggests two (not mutually exclusive) possibilities: 1) the decline in activation was not representative of decay, so it did not correlate with performance, or 2) these regions might not have been storage regions (but see Todd & Marios, 2004; Xu & Chun, 2006 for evidence more supportive of load sensitivity in posterior regions).

The idea that neural activity decays also faces a serious challenge from the classic results of Malmö (1942), who found that a monkey with frontal lesions was able to perform a delayed response task extremely well (97% correct) if visual stimulation and motor movement (and therefore associated interference) were restricted during a 10-second delay. By contrast, in unrestricted conditions, performance was as low as 25% correct (see also Postle and D'Esposito, 1999). In summary, evidence for time-based declines in neural activity that would naturally be thought to be part of a decay process is mixed.

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3.1.3 Is there a mechanism for decay? At least two key empirical results (McKone, 1998; Harris, 1952) do seem to implicate some kind of time-dependent decay. If one assumes that decay happens, how might it occur?

One possibility—perhaps most compatible with results like those of Malmö (1942)—is that what changes over time is not the integrity of the representation itself, but the likelihood that attention will be attracted away from it. This explanation is also compatible with the focus-of-attention view of STM. By this explanation, the representation within the focus does not decay. However, as more time passes, there is a greater likelihood that attention is attracted away from this representation and toward external stimuli or other memories.

For recently-presented items outside of the focus, decay may occur because of stochastic variability in the activity of the neurons that make up an item's representation. The temporal synchronization of neuronal activity is an important part of the representation (e.g., Deiber et al., 2007; Jensen, 2006; Lisart & Idiart, 1995), and it is possible that being in the focus helps to maintain this synchrony. As time out of the focus increases, variability in the firing rates of individual neurons may cause them to fall increasingly out of synch, unless they are reset by rehearsal. By this hypothesis, as the neurons fall out of synchrony, the pattern of activation that forms the representation becomes increasingly difficult to discriminate from surrounding neural noise [see Lustig, Matell, & Meck, 2005 for an example that integrates neural findings with computational (Frank et al., 2001) and behaviorally-based (Brown et al., 2000) models of STM].

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3.2 Interference theories: Comprehensive but complex

Interference effects play several roles in memory theory: First, they are the dominant explanation of forgetting. Second, some have suggested that STM capacity and its variation among individuals is largely determined by the ability to overcome interference (e.g., Hasher & Zacks, 1988; Unsworth and Engle, 2007). Finally, differential interference effects in short- and long-term memory have been used to justify the idea that they are separate systems, and common interference effects have been used to justify the idea that they are a unitary system.

Interference theory has a problem opposite that of decay: It is comprehensive but complex (Crowder, 1976). The basic principles are straightforward. Items in memory compete, with the amount of interference determined by the similarity, number, and strength of the competitors. The complexity stems from the fact that interference may occur at multiple stages (encoding, retrieval, and possibly storage) and at multiple levels (the representation itself, or its association with a cue or a response). Interference from the past (proactive interference, PI) may affect both the encoding and the retrieval of new items, and it often increases over time. By contrast, interference from new items onto older memories (retroactive interference, RI) frequently decreases over time, and may not be as reliant on similarity (see discussion by Wixted, 2004).

3.2.1 Retrieval interference. It can be difficult to select between items that are similar to each other. For example, if participants learn and recall four lists from the same category (e.g., "flowers"), recall performance shows typical PI effects: decreasing performance across the lists. However, if the category of the fourth list is changed, even subtly (e.g., "wildflowers") memory for this list can be nearly as high as on the very first trial (Wickens, 1970). Importantly, this "release from PI" occurs even if the subject is only made aware of the category shift *after* the list has been learned (Gardiner et al., 1972). This suggests that the effects of category-change occur largely at retrieval, by helping participants differentiate and thus select recent-list items from others in memory.

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Comment: Rick suggested changing this to "retrieval interference" rather than "selection-based interference". I changed it back because we include the response interference here, too...and I'm not sure that one would necessarily call that "retrieval interference" per se. But if others feel differently, then I'm ok with the change.

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Comment: I slightly prefer selection-based interference for the reasons Cindy suggested, but what I like about Rick's title is that we actually talk about retrieval as a term, and I think it works as well (in other words, I'm ok with the change, even if I prefer the original a bit.)

Selection and retrieval processes remain an important topic in interference research. Functional neuroimaging studies consistently identify a region in left inferior frontal

gyrus (LIFG) as active during interference-resolution, at least for verbal materials (see a review by Jonides & Nee, 2006). This region appears to be generally important for selection among competing alternatives, e.g., in semantic memory as well as in STM (Thompson-Schill et al., 1997). In STM, LIFG is most prominent during the test phase of interference trials, and its activation during this phase often correlates with behavioral measures of interference-resolution (Jonides et al., 1998; D'Esposito et al., 1999; Reuter-Lorenz et al., 2000; Thompson-Schill et al., 2002). These findings attest to the importance of processes for resolving retrieval interference. The commonality of the neural substrate for interference-resolution across short-term and long-term tasks provides yet further support for the hypothesis of shared retrieval processes for the two types of memory.

Interference effects occur at multiple levels and it is important to distinguish between interference at the level of representations and interference at the level of responses. The LIFG effects described above appear to be familiarity-based and to occur at the level of representations. Items on a current trial must be distinguished and selected from among items on previous trials that are familiar because of prior exposure, but are currently incorrect. A separate contribution occurs at the level of responses: An item associated with a positive response on a prior trial may now be associated with a negative response, or vice versa. This response-based conflict can be separated from the familiarity-based conflict, and its resolution appears to relate more to activity in the anterior cingulate (Nelson et al., 2003).

3.2.2 Other mechanisms for interference effects? Many studies examining encoding in STM have focused on retroactive interference (RI): how new information disrupts previous memories. Early theorists described this disruption in terms of displacement of entire items from STM, perhaps by disrupting consolidation (e.g., Waugh & Norman, 1965). However, rapid serial visual presentation (RSVP) studies suggest that this type of consolidation is complete within a very short time – less than 500ms, and in some situations as short as 50ms (Vogel et al., 2006).

What about interference effects beyond this time window? As reviewed above, most current focus-based models implicitly assume something like whole-item displacement is at work. It is not clear how these models account for similarity-based interference. Two recent models (Nairne, 2002; Oberauer, 2006) suggest a possible modification. Rather than a competition at the item-level for a single-focus resource, these models posit a lower-level similarity-based competition for “feature units.” By this idea, representations are composed of bundles of features (e.g., color, shape, spatial location, temporal location), which are in turn distributed over multiple units. The more two items overlap, the more they compete for these feature units, resulting in greater interference. This proposed mechanism fits well with the idea that perception, STM, and LTM rely on representations that are distributed throughout sensory, semantic, and motor cortex (Postle, 2006). As we describe next, it is also congruent with the stochastic mechanism we suggested earlier for decay.

3.3 Interference-based decay?

The mechanism we earlier proposed for decay is based on the idea that stochastic variability causes the neurons making up a representation to fall out of synchrony. Using the terminology of Nairne (2002) and Oberauer (2006), the feature units become less tightly bound. Feature units that are not part of a representation also show some random activity due to their own stochastic variability, creating a noise distribution. Over time, there is an increasing likelihood that the feature units making up the to-be-remembered item's representation will overlap with those of the noise distribution, making them increasingly difficult to distinguish. This increasing overlap with the noise distribution and loss of feature-binding could lead to the smooth forgetting functions often interpreted as evidence for decay.

Interestingly, such a mechanism could also account for strength-of-learning effects and similarity-based interference. Poorly learned items might have fewer differentiating features and be less tightly bound, thus making their representations more difficult to discriminate from the noise distribution to begin with, and faster to lose their integrity by falling out of synchrony. In fact, McKone (1998) found that non-words decayed faster than words, and were also more susceptible to interference. In summary, although it is speculative, this model of neural representations and how they change over time due to intrinsic variability in neuronal activity supplies a unified mechanism for interference and decay.

4. A sketch of short-term memory at work

In our review, we have tried to bring together the literature on behavioral and neuroscience data concerned with short-term memory. Here, we sketch out how this integration might work on a moment-to-moment basis throughout a typical STM task: an n-back probe recognition task.

Figure 5 illustrates the task events in terms of the stimulus display and the subject's response. The stages of the task are displayed in a more abstract form in Figure 6, with the task events at the bottom of the figure and the putative cognitive events at the top. In the task, the participant sees a letter presented for 700ms and must respond 'yes' if the letter matches a letter seen 4-back, and respond 'no' if the letter does not match the letter 4-back. Therefore in this task, the participant must actively maintain 4 items to match the current probe against the 4-back item. The participant must also keep track of the other items for future trials.

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Comment: Actually McKone's data do not show that. McKone shows that non-words decay faster than words, and non-words are also more susceptible to interference than words. In addition, McKone found that interference from other items was stronger than time-based decay.

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Comment: Isn't the strongest prediction of this view an interaction of decay (time) and interference (similarity)? Decay is worse the more similar the items are. What is the clearest evidence for this? CL: Isn't McKone's data consistent with this idea?

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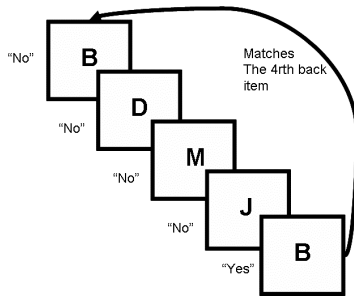


Figure 5: Sample STM task: The N-Back task (where N = 4)

We adopt the STM architecture of Oberauer (2002) along with our elaboration of the processes involved in STM and forgetting to explain how this task would be accomplished.

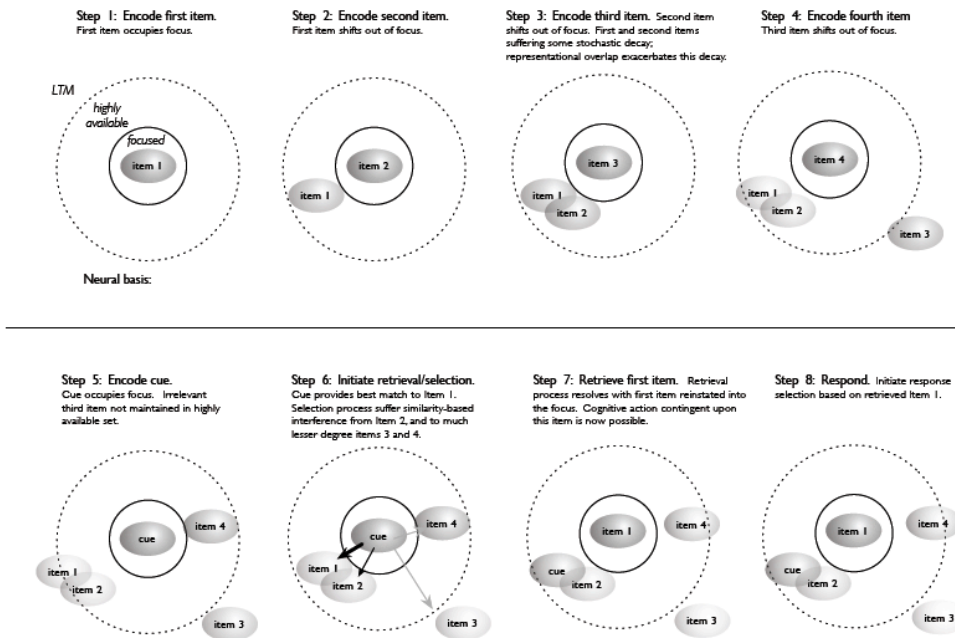


Figure 6: Model of STM performing the N-back task.

To reiterate, the focus of attention consists of frontal and parietal regions biasing posterior cortical areas that are involved in perception and storage of LTM representations. Items outside the focus are either in a highly accessible state, or are more dormant in these representational cortices.

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In this task, shown in Figure 5, the participant first encodes the letter 'B', activating posterior perceptual areas, presumably in left inferior temporal cortex (Polk et al., 2002). This item moves into the focus of attention, and the MTL initiates its contextual binding. 'B' does not match the 4-back item, so the subject responds "No". Next, the letter 'D' is shown, which displaces the letter 'B' from the focus of attention when 'D' is encoded using the same process as described for 'B'. The participant must still keep the letter 'B' active, even though it is not the focus of attention, and thus it remains in a highly active state outside the focus of attention. MTL activation persists for 'B', maintaining the item's context; however, this activation is greatly decreased due to stochastic drift as outlined above, possibly leading to decay of the representation. This process continues for the rest of the items. The participant responds with "no" to the first four items ('B', 'D', 'M', and 'J'), as they do not match the letter 4-back. Moreover, each item displaces the previous item from the focus of attention. In addition, throughout the task, the participant rehearses the items, which periodically brings the items that are out of the focus back into the focus. Frontal and parietal areas increase biasing in the posterior regions to retrieve these items back into the focus during rehearsal. And rehearsal itself is mediated by premotor and inferior frontal gyrus regions. Finally, the participant gets the letter 'B', which does match the item 4-back.

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Before we move on to the retrieval process, notice the following depicted in figure 6. First, the representations of items 1 and 2 (B and D) overlap due to their featural and contextual similarities (shape, phonology, and temporal context). Second, items 3 and 4 (M and J) are much farther away from items 1 and 2. This is because these items do not share many features with items 1 and 2. In addition, item 3 is no longer within the activated/highly available state. This item has suffered from proactive interference from items 1 and 2 and retroactive interference from item 4. In addition to this interference, this item has also lost representational fidelity due to stochastic decline in neural firing when it was not in focus.

When the cue letter B is presented, the participant performs a cue-based retrieval of that item. The cue best matches item 1, but it also may be subject to some similarity-based interference from item 2, which could induce an incorrect response or delay the correct response, "yes." There is also similarity-based interference from items 3 and 4, but this interference is much weaker. Item 1 is then brought back into the focus, replacing the cue, and the participant responds affirmatively.

4. Principles of short-term memory

Let us step away from this particular example and take stock of what we now know about short-term memory, both the psychological and the neural mechanisms. Our review of the structure, processes, and forgetting mechanisms of STM lead us to the following synthesis of the facts of the matter.

4.1 Psychological Mechanisms of Short-term Memory

- The core of short-term memory is a focus of attention containing a single functional context and the items bound within it.
- The representations that the focus of attention operates on in STM are isomorphic with those that form the basis of initial perception and storage in LTM.
- These focused representations consist of bundles of features for stored information. Those features can include those that tie an item to its functional context—for example, serial order, time, or location—and novel relations among familiar items.
- Representations enter the focus of attention via perceptual encoding or via cue-based retrieval from LTM.
- Controlled, active maintenance processes are required to keep a representation in the focus.
- Rehearsal is not a core STM maintenance process, in that it does not keep a representation consistently within the focus. Instead, it consists of controlled but sequential retrieval of highly-activated but out-of-focus LTM representations into the focus.
- Forgetting occurs when the fidelity of a representation declines over time due to stochastic processes (“pure” decay), or because of similarity-based competition between representations for features (interference-based decay). Similarity also influences competition between representations for the focus of attention (retrieval or selection-based interference).

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4.2 Neural Mechanisms of Short-term Memory

- Frontal and parietal systems mediate the control of the focus of attention by their connections with and modulations of activity in posterior regions that represent the features of representations within the focus.
- The (largely posterior) systems that represent item features for perception, action, or LTM storage also represent those features for STM. Items within the focus of attention are represented by patterns of heightened, synchronized firing of neurons in these (verbal, spatial, motor, etc) regions.
- Medial temporal structures are important for binding items to their context (including information about time and spatial location), and for retrieving items

whose context is no longer in the focus of attention (an STM function) or fully consolidated in neocortex (an episodic LTM function).

- The inherent variability of neuronal activity may contribute to the loss of integrity of neural representations, and thus lead to forgetting.

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