

Neuroscientific Evidence About the Distinction Between Short- and Long-Term Memory

Derek Evan Nee, Marc G. Berman, Katherine Sledge Moore, and John Jonides

University of Michigan

ABSTRACT—*What have neuroscientific techniques contributed to the development of psychological theory about short- and long-term memory? We argue that the contributions have been varied: In some cases, data about brain mechanisms have been vital to the advancement of psychological theory; in other cases, neuroscientific data and behavioral data from normal participants have made equal contributions; and in yet other cases, the data from neuroscientific approaches have actually led psychological theory astray. We illustrate these various contributions by focusing on the relationship of short- to long-term memory.*

KEYWORDS—*short-term memory; long-term memory; neuroimaging; neuroscience; double dissociation*

Is human memory unitary, or are there qualitatively different memory systems that contribute to cognitive functioning? This fundamental question has vexed psychologists since the insightful discussions of William James in 1890. The issue turns on whether there are dissociable systems for handling the encoding, storage, and retrieval of information for short versus long retention durations. James argued that “primary” (or short-term) memory (STM) had features distinguishing it from “secondary” (or long-term) memory (LTM). The contrasting position is that there is but a single memory system that obeys similar principles of encoding, storage, and retrieval regardless of retention interval. This issue rages to this very day.

What contribution have neuroscientific data made to our understanding of whether memory is singular in architecture or the result of multiple systems? We focus on the distinction between STM and LTM because we believe that neuroscientific data have been particularly influential about this issue. That influence has

manifested itself in three ways. First, neuropsychological work and work with nonhuman primates originally suggested different neural architectures for STM and LTM, leading to psychological theories that differentiated these memory systems. However, reinterpretations of these data suggest that the original findings may have been misleading. Second, in many cases, neural data have converged with behavioral data, leading to strengthening of existing cognitive theory. Third, important experiments studying the neural basis of memory representations have demonstrated that the neural substrates of perception, LTM, and STM are highly overlapping, lending support to unitary theories of memory. We illustrate each of these influences in our brief review.

Notably, we focus on neuroscience’s influence on psychology. We take it as a given that psychology has been extremely influential in studies of the neuroscience of memory. For example, of the studies that include “short-term memory” and “fMRI” (functional magnetic resonance imaging) or “PET” (positron-emission tomography) in their titles or abstracts, approximately one third cite Baddeley’s psychological model of short-term memory (e.g., see Baddeley, 2003). Hence, we believe that psychology’s influence on neuroscience is clear; thus we choose instead to review neuroscience’s influence on psychology.

THE INFLUENCE OF NEUROSCIENCE ON MULTI-STORE MODELS OF MEMORY

One of the most fundamental questions examined by memory theorists is whether STM is qualitatively distinct from LTM, or whether STM and LTM can be represented along a single quantitative continuum. Although some of the earliest accounts of memory assumed the former, by the 1960s some theorists called the STM/LTM dichotomy into question (e.g., Melton, 1963). These unitary views of memory were supported by similar forms of forgetting and susceptibility to interference present in both STM and LTM.

Address correspondence to Derek Evan Nee, Department of Psychology, University of Michigan, 530 Church Street, Ann Arbor, MI 48109-1043; e-mail: dneee@umich.edu.

Neuroscience influenced this debate with data from neuropsychological case studies. On the one hand, patients with damage to the medial temporal lobe (MTL) demonstrated deficits in LTM, whereas their ability to hold information online during the short term was intact (Scoville & Milner, 1957). On the other hand, patients with damage to perisylvian cortex demonstrated a profound deficit in maintaining short-term phonological information, yet their LTM remained intact (Shallice & Warrington, 1970). This double dissociation provided support to models distinguishing STM and LTM.

Further influential work came from studies of nonhuman primates. Lesions of the inferior temporal (IT) cortex produced specific deficits in visual discrimination learning, suggesting that IT may store long-term representations of visual stimuli (Gross, 1972). In addition, Goldman-Rakic and colleagues found that frontal cells fired continuously during the retention interval of a STM task and that these neurons responded to specific stimuli, suggesting that the frontal cortex may be the locus of short-term storage (e.g., Funahashi, Bruce, & Goldman-Rakic, 1989). Piecing these results together, Miller, Erickson, and Desimone (1996) examined both frontal and IT neurons during an STM task that included distracting stimuli during the retention interval. Like Goldman-Rakic and colleagues, this study found stimulus-selective frontal activity that spanned the retention interval, even in the face of distraction. These results contrasted with recordings from IT sites whose activity was abolished following the presentation of distracting stimuli. Taken together, these findings implied a frontally mediated short-term store that is distinct from posterior regions that hold LTM representations.

Substantial behavioral research has also contributed to the STM/LTM distinction. In one classic study, subjects were presented with lists of 20 words and were told to recall as many words as possible in any order (Glanzer & Cunitz, 1966). In paradigms such as these, subjects typically demonstrate superior memory for items at the beginning of the list relative to the middle (the primacy effect), as well as superior memory for items at the end of the list relative to the middle (the recency effect). The primacy effect is presumed to reflect the contribution of LTM, whereas the recency effect is presumed to reflect the contribution of STM. Glanzer and Cunitz (1966) used the logic of double dissociation to demonstrate that these stores were separable. That is, they reasoned that if one variable affected LTM but not STM, and another variable affected STM but not LTM, that this would provide strong evidence that STM and LTM constituted separate memory systems. Whereas a slowed presentation rate increased the primacy effect—presumably by giving subjects more time to rehearse items and form LTM traces—this did not modify the recency effect. By contrast, increasing the delay between the end of the list presentation and recall reduced the recency effect, presumably because recent items were forgotten from STM during the delay; this manipulation, however, did not alter the primacy effect. This pattern of results provided behavioral signatures for separate stores.

Recent neuroimaging work has supported this dissociation, albeit somewhat redundantly to previous behavioral research. To examine the neural correlates of the serial-position effects, Talmi, Grady, Goshen-Gottstein, and Moscovitch (2005) presented subjects with a list of 12 items followed by a recognition probe. The critical contrast was between recognition probes of early-presented items (positions 1 and 2) and probes of late-presented items (positions 11 and 12). Presumably, early probes require retrieval from LTM, whereas late probes require retrieval from STM. These authors found MTL activation for early, but not late, probes, and right inferior parietal activation for late, but not early, probes. This pattern of double dissociation confirmed the behavioral findings from the serial-position tasks, lending support to multi-store models of memory.

In summary, neuroscience has exerted a powerful influence on psychological theories of memory, having led many theorists to adopt multi-store models. Many of these theories discuss not only the psychological mechanisms underlying STM and LTM but also their neural correlates (e.g., see Baddeley, 2003). Although the neuroscientific evidence suggesting distinct short- and long-term memory stores has greatly influenced psychology, we turn now to data suggesting that this evidence may have been misleading.

THE INFLUENCE OF NEUROSCIENCE ON UNITARY-STORE MODELS OF MEMORY

Multi-store models of STM and LTM rest upon neuroscientific data suggesting the importance of the MTL for long-term but not short-term storage and the importance of frontal and perisylvian cortices to short-term but not long-term storage. Recent findings call this idea into question, however. Ranganath and Blumenfeld (2005) reviewed evidence demonstrating that short-term storage can be disrupted by damage to the MTL. They explained that when the information to be stored is novel, patients with MTL lesions show profound deficits in short-term retention. These data are corroborated by both neuroimaging and single-unit recordings in nonhuman primates demonstrating sustained MTL activity during the delay periods of short-term retention tasks (see Ranganath & Blumenfeld, 2005, for a review). These results suggest that, rather than being unique to LTM, the MTL binds together novel information into a single representation. This binding function helps mediate representations for successful STM and LTM performance. The degree to which the MTL is recruited for short-term performance is therefore likely to rely on the novelty of the material and on the degree to which the task necessitates binding. Therefore, the discrepancy of these findings with earlier data may be attributed to differences in the tasks used to assess STM.

As we reviewed, early theories regarded the frontal cortex as the site of STM storage, separate from LTM storage. However, more recent theories call this proposal into question (e.g., Postle, 2006; Ranganath & Blumenfeld, 2005). These theories rely on

evidence demonstrating that patients with large frontal-lobe lesions show normal performance on span tasks that require subjects to maintain information for only a brief period (D'Esposito & Postle, 1999). Also, nonhuman primates with frontal lesions can perform short-term retention tasks, provided the environment has minimal distractions (Malmo, 1942). These results have led to the hypothesis that the frontal cortex supports resistance to distraction rather than supporting storage itself (Postle, 2006; Ranganath & Blumenfeld, 2005).

Finally, although patients with perisylvian damage are characterized by short-term memory deficits but not long-term ones, these results may derive from phonological deficits rather than memory deficits per se. For example, left perisylvian damage results not only in STM deficits but in general deficits in phonological processing (Martin, 1993). The observed differences in STM and LTM may therefore have to do with differences in stimulus materials used to test these patients: Whereas the LTM tasks generally relied on material that can be encoded semantically (e.g., words), the STM tasks often relied on materials that cannot (e.g., digits). Supporting this idea, patients with perisylvian damage also show impaired LTM for auditorally presented nonwords that cannot be encoded visually or semantically (Ranganath & Blumenfeld, 2005). Hence, perisylvian damage does not appear to produce deficits unique to STM; rather, it produces general phonological deficits that can also affect LTM.

These data converge on a view that storage operations of STM and LTM are not as dissimilar as was once thought, calling theories distinguishing these memory systems into question. However, if there is just one kind of memory, how can it be characterized? Recent neuroimaging studies are beginning to shed light on this question.

Sakai, Rowe, and Passingham (2002) examined maintenance activity during a spatial-STM task. In this study, subjects maintained 5 spatial locations over a short interval that included a spatial-distraction task. The authors found sustained activity during the retention interval in frontal and more posterior regions thought to be responsible for spatial representations (the frontal eye fields, FEF, and intraparietal sulcus, IPS). Interestingly, frontal activation was maintained only during correct trials, and greater frontal activity predicted a stronger correlation between activations in the FEF and IPS. By contrast, frontal activation was absent during error trials, consistent with decreased correlation between the FEF and IPS. These results suggest that the frontal cortex produces distractor-resistant maintenance in posterior areas.

In a complementary way, Fiebach, Rissman, and D'Esposito (2006) examined mechanisms of short-term verbal storage. These authors began by determining the region of the cortex responsible for representing visually presented words (i.e., the visual-word-form area). They then explored activation in this region during the retention interval while subjects maintained either 2 or 5 words or pronounceable pseudowords in STM. The

visual-word-form area showed increased activation when subjects maintained 5 words, compared to 2 words, but it did not show this pattern for pseudowords. Additionally, activation in the visual-word-form area correlated with frontal cortex activation, and this correlation was greater for 5 words compared to 2 words and greater for words compared to pseudowords. Pseudowords, by contrast, exhibited more robust activations compared to words in regions thought to correspond to phonological rehearsal, activating more for 5 than for 2 pseudowords. This suggests a reliance on phonological processes to create and maintain a novel representation of pseudowords.

In both of these studies, areas of the cortex responsible for representing a particular type of information (FEF and IPS for locations, visual-word-form area for words) are critical for short-term maintenance. Loss of correlations between representational areas corresponds to error-prone performance (Sakai et al., 2002), and activation in representational areas increases with increased memory load (Fiebach et al., 2006). Furthermore, the frontal cortex appears to be inextricably tied to successful maintenance in these representational areas. Finally, when no prior representation exists, alternative maintenance processes appear to be recruited.

These data have influenced and refined unitary models of memory. For example, Postle (2006) has proposed that the same regions of the brain that represent sensation and action have evolved to support both the sensory and motoric aspects of memory. By this account, what constitutes STM is simply attentionally mediated activation of these LTM representations (see also Cowan, 2001). Therefore, STM and LTM do not differ in representations; rather, they differ in activation, which is mediated by attention. This attentional mediation is thought to depend critically on frontal biasing of posterior representational cortices. This account fits well with the Sakai et al. (2002) and Fiebach et al. (2006) studies reviewed above (see Postle, 2006, for additional evidence).

Beyond questions of storage, there is evidence for similar processes of retrieval from both STM and LTM. A meta-analysis examining neuroimaging activations of long-term episodic retrieval and STM retrieval revealed similar lateral frontal involvement for both processes (Cabeza, Dolcos, Graham, & Nyberg, 2002). To add support for this claim, Cabeza et al. (2002) examined episodic long-term retrieval and short-term retrieval in the same subjects using event-related fMRI. In the episodic retrieval task, subjects compared a probe to a list studied before scanning and judged whether they remembered the item, knew it as familiar, or had not seen it before. In the short-term retrieval task, subjects studied a 4-item list and made a yes/no response to a probe appearing 12 seconds later. The authors found overlapping left-lateral frontal activations for both types of retrieval, suggesting similarities in retrieval for STM and LTM. However, both the meta-analysis and the empirical study found unique anterior frontal recruitment for long-term episodic retrieval. One possibility for this pattern is that in the episodic long-term task,

there is a need to inspect specific details about the retrieved information to make a “remember” judgment. This monitoring of recollected details is unnecessary for simple recognition in the short-term task. Therefore, common left-lateral frontal activation may reflect retrieval, whereas the anterior prefrontal activation may reflect monitoring processes acting upon this retrieved information.

Consonant with this idea, Badre and Wagner (2005) examined regions involved in resolving proactive interference in STM. Like Cabeza et al. (2002), these authors used a verbal short-term item-recognition task. However, their study was different in that some of the recognition probes were members of the *previous* memory set (recent items; see Jonides & Nee, 2006, for a review of similar procedures). These recent items could either be present in the current memory set (recent positives requiring a “yes” response) or absent from it (recent negatives requiring a “no” response). Hence, whereas recent presentation of an item generally facilitates correct responding in typical short-term tasks, here this information can mislead subjects during recent negative trials. Therefore, in this task, subjects must monitor retrieved information to determine its source and not simply rely on item familiarity. Supporting the idea that anterior prefrontal activation reflects this monitoring process, the authors found greater left anterior prefrontal activation for recent items compared to nonrecent items. Additionally, recent items produced greater left-lateral frontal activation than nonrecent items did, as would be expected if this region plays a role in retrieving information. To establish that these regions were not unique to STM, the authors compared these activations to regions found in a previous study examining the neural correlates of episodic recollection of specific details. This comparison yielded a great deal of overlap in both the lateral and anterior frontal cortex, suggesting that common retrieval mechanisms are involved in both STM and LTM.

CONCLUSION

Just as the neuroscientific study of memory owes its inspiration to psychology, psychological theories of memory have relied greatly upon data from neuroscience. As we have argued here, the evolution of psychological theories has been influenced by the findings of neuroscience. This influence may have originally provided misleading evidence for multi-store views of memory, but more recent work provides important support for unitary views of memory. Although this debate is far from over, it will likely continue to rely on neuroscience to refine, support, and reject psychological theories of memory.

Recommended Reading

Cowan, N. (2001). (See References). Provides a comprehensive review of STM capacity.

- Jonides, J., Lacey, S.C., Nee, D.E. (2005). Processes of working memory in mind and brain. *Current Directions in Psychological Science*, *14*, 2–5. Article in which we argue that regions involved in perceiving a particular type of information are also involved in maintaining that information over the short term, and that rehearsal engages the same regions that control attention to external stimuli.
- Jonides, J., Lewis, R.L., Nee, D.E., Lustig, C.A., Berman, M.G., & Moore, K.S. (2008). The mind and brain of short-term memory. *Annual Review of Psychology*, *59*, 193–224. A review of recent psychological and neural developments in STM.
- Postle, B.R. (2006). (See References). Examines evidence that storage functions of STM involve sensory-, representation-, and action-related regions.
- Ranganath, C. and Blumenfeld, R.S. (2005). (See References). A review that reconsiders the traditional STM/LTM distinction, providing a more in-depth look at some of the points raised in the current article.

REFERENCES

- Baddeley, A. (2003). Working memory: Looking back and looking forward. *Nature Reviews Neuroscience*, *4*, 829–839.
- Badre, D., & Wagner, A.D. (2005). Frontal lobe mechanisms that resolve proactive interference. *Cerebral Cortex*, *15*, 2003–2012.
- Cabeza, R., Dolcos, F., Graham, R., & Nyberg, L. (2002). Similarities and differences in the neural correlates of episodic memory retrieval and working memory. *Neuroimage*, *16*, 317–330.
- Cowan, N. (2001). The magical number 4 in short-term memory: A reconsideration of mental storage capacity. *Behavioral and Brain Sciences*, *24*, 87–185.
- D’Esposito, M., & Postle, B.R. (1999). The dependence of span and delayed-response performance on the prefrontal cortex. *Neuropsychologia*, *37*, 1303–1315.
- Fiebach, C.J., Rissman, J., & D’Esposito, D.E. (2006). Modulation of inferotemporal cortex activation during verbal working memory maintenance. *Neuron*, *51*, 251–261.
- Funahashi, S., Bruce, C.J., & Goldman-Rakic, P.S. (1989). Mnemonic Coding of Visual Space in the Monkey’s Dorsolateral Prefrontal Cortex. *Journal of Neurophysiology*, *61*, 331–349.
- Glanzer, M., & Cunitz, A.R. (1966). Two storage mechanisms in free recall. *Journal of Verbal Learning and Verbal Behavior*, *5*, 351–360.
- Gross, C.G. (1972). Visual functions of inferotemporal cortex. In R. Jung (Ed.), *Handbook of sensory physiology* (pp. 451–482). Berlin: Springer.
- Jonides, J., & Nee, D.E. (2006). Brain mechanisms of proactive interference in working memory. *Neuroscience*, *139*, 181–193.
- Malmö, R. (1942). Interference factors in delayed response in monkeys after removal of frontal lobes. *Journal of Neurophysiology*, *5*, 295–308.
- Martin, R.C. (1993). Short-term memory and sentence processing: Evidence from neuropsychology. *Memory and Cognition*, *21*, 176–183.
- Melton, A.W. (1963). Implications of short-term memory for a general theory of memory. *Journal of Verbal Learning and Verbal Behavior*, *2*, 1–21.

- Miller, E.K., Erickson, C.A., & Desimone, R. (1996). Neural mechanisms of visual working memory in prefrontal cortex of the macaque. *Journal of Neuroscience*, *16*, 5154–5167.
- Postle, B.R. (2006). Working memory as an emergent property of the mind and brain. *Neuroscience*, *139*, 23–38.
- Ranganath, C., & Blumenfeld, R.S. (2005). Doubts about double dissociations between short- and long-term memory. *Trends in Cognitive Sciences*, *9*, 374–380.
- Sakai, K., Rowe, J.B., & Passingham, R.E. (2002). Active maintenance in prefrontal area 46 creates distractor-resistant memory. *Nature Neuroscience*, *5*, 479–484.
- Scoville, W.B., & Milner, B. (1957). Loss of recent memory after bilateral hippocampal lesions. *Journal of Neurological and Neurosurgical Psychiatry*, *20*, 11–21.
- Shallice, T., & Warrington, E.K. (1970). Independent functioning of verbal memory stores: A neuropsychological study. *Quarterly Journal of Experimental Psychology*, *22*, 261–273.
- Talmi, D., Grady, C.L., Goshen-Gottstein, Y., & Moscovitch, M. (2005). Neuroimaging the serial position curve. *Psychological Science*, *16*, 716–723.