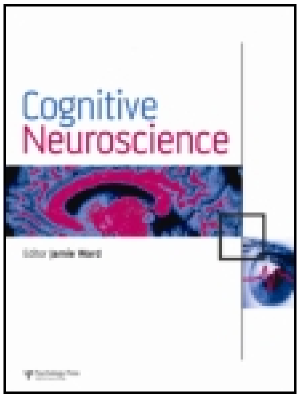

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The cognitive neuroscience of memory

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Introduction

The cognitive neuroscience of memory

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The cognitive neuroscience of long-term memory is ingrained with the assumptions that a particular task measures a single cognitive process and that each cognitive process is mediated by a single brain region. However, these assumptions are simplistic and hindering progress toward understanding the true mechanisms of memory. This special issue of *Cognitive Neuroscience* presents five empirical papers and two theoretical discussion papers with peer commentaries on the spatial and/or temporal mechanisms of memory. Using fMRI, Yu et al. show ventral parietal cortex sub-regions mediate dissociable aspects of recollection, and Mickley Steinmetz et al. study time-delay effects on processes engaged during emotional versus neutral item encoding. Employing ERPs, Galli et al. investigate anticipatory activity and recall, and Evans et al. study the effect of cognitive demands on recollection activity. Using fMRI and ERPs, Herzmann et al. investigate spatial-temporal activity associated with recognition. Voss et al. review electrophysiological, fMRI, and behavioral evidence indicating implicit memory can influence explicit memory measures. Gotts et al. review electrophysiological, fMRI, and modeling evidence to evaluate proposals of repetition priming and highlight neural synchronization. These papers embrace complex cognitive and neural processes, and thus will provide a framework for future studies to investigate the mechanisms of memory.

Keywords: Explicit memory; Implicit memory; Recollection; Familiarity; Mechanisms; fMRI; ERPs; Review.

Long-term memory refers to the encoding or retrieval of information that is mediated by conscious or nonconscious processing. Perhaps due to the inherent complexity of this topic, the cognitive neuroscience of memory is fraught with simplifying assumptions. For instance, explicit/direct memory tasks (such as old-new recognition) are widely assumed to measure conscious processing, while implicit/indirect memory tasks (such as repetition priming) are widely assumed to measure nonconscious processing. In addition, the "remember"-"know" task is generally thought to dissect explicit memory into recollection (measured by "remember" responses) and familiarity (measured by "know" responses). However, the cognitive processes mediating such tasks are not pure. Both conscious and nonconscious processes operate, to some degree, during explicit and implicit tasks, and recollection and familiarity often co-occur.

Cognitive neuroscientists also assume that particular mental processes are associated with specific brain regions. This is illustrated by a few (of the numerous) examples from the field of memory—the hippocampus and the perirhinal cortex have been associated with recollection and familiarity, respectively, the ventral lateral parietal cortex has also been associated with recollection, and the prefrontal cortex has been linked to post-retrieval monitoring. Such process-to-region mappings are reminiscent of phrenology (Uttal, 2003; for an excellent review of phrenology, a pseudoscience developed by Franz Joseph Gall over two centuries ago, see van Wyhe, 2004). The current modular view of brain function can be attributed to our overreliance on functional magnetic resonance imaging (fMRI), a

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method which typically produces a very limited number of brain activations that are assumed to mediate a particular cognitive process. However, there is no evidence for the existence of independent cognitive processing modules in the brain (the opposite is true—multiple brain regions are known to interact during any cognitive process), and such a static modular view implies temporal aspects of processing are unimportant (which is also unequivocally false) (Slotnick, in press). Regarding the latter point, fMRI measures brain activity in seconds, but the brain operates in milliseconds; therefore, this technique cannot be used in isolation to study the spatial-temporal dynamics of the functioning brain.

Although adhering to one-to-one task-to-process and process-to-region mappings has historically provided some insight into memorial processing, such simplistic assumptions are presently hindering progress toward understanding the true mechanisms of memory. The papers in this special issue of *Cognitive Neuroscience* challenge many assumptions that are currently (mis)guiding the large majority of research on memory.

The first two empirical papers in this special issue use fMRI to isolate neural activity associated with specific cognitive processes. Yu, Johnson, and Rugg show that activity in the angular gyrus varies as a function of recollection confidence, while activity in the temporal parietal junction corresponds to recollection independent of confidence. This suggests there are different forms of recollection associated with particular sub-regions of the ventral lateral parietal cortex. Mickley Steinmetz, Schmidt, Zucker, and Kensinger investigate the effect of a 0.5 or a 24 hour study-to-test time delay on the neural processes engaged during emotional item encoding versus neutral item encoding. They find that for neutral items the correspondence of encoding activity to subsequent memory performance is stronger at the short delay than the long delay, but for emotional items the correspondence is at least as strong at the long delay as compared to the short delay. This illustrates that varying study-to-test delay can be used to gain insight into the neural processes mediating different forms of memory. Of importance, rather than simply using fMRI to identify regions of activity associated with popular tasks and presumed underlying cognitive processes, the two previous fMRI studies use more complex experimental protocols to uncover novel characteristics of memory.

The next three empirical papers in this special issue use event-related potentials (ERPs) to investigate the time course of memorial processing. Galli, Choy, and Otten study the relationship between anticipatory activity—500 milliseconds before the onset of visual words or auditory words during elaborative encoding or rote encoding—and subsequent recall. They find that frontal activity preceding auditory words during elaborative encoding predicts later recall, which suggests semantic anticipatory processes are particularly important for encoding these items. Evans, Herron, and Wilding manipulate item spatial location (left visual field or right visual field) and task (animate/inanimate judgments or pleasant/unpleasant judgments) during encoding, and then during retrieval a "location" cue or a "task" cue dictates the appropriate response for each item. They find that the magnitude of left parietal hit versus correct rejection activity 500–800 milliseconds after onset (i.e., the left parietal old-new recognition effect) is larger for repeated than non-repeated cues/trials. These results show that cognitive demands can influence the left parietal old-new recognition effect, an index of episodic detail/recollection. It is notable that the previous ERP findings would have been difficult, if not impossible, to track using fMRI due to the rapid temporal dynamics of these effects. Herzmann, Jin, Cordes, and Curran combine fMRI and ERPs in the same participants to investigate spatial-temporal activity associated with object recognition. The ERP memory components they evaluate include frontal activity that occurs 300–500 milliseconds following cue onset (the FN400) thought to reflect familiarity, parietal activity that occurs 500–800 milliseconds following cue onset thought to reflect recollection (the left parietal old-new recognition effect mentioned above; Evans et al.), and frontal activity that occurs 800 milliseconds or later following cue onset believed to reflect post-retrieval monitoring. This study evaluates recognition activity separately during fMRI and ERPs and also elucidates the relationships between the results obtained using these two techniques. By employing ERPs, the previous three studies investigate the rapid neural processes that mediate memory.

The two review papers in this issue evaluate a wealth of recent evidence and challenge commonly held beliefs regarding the cognitive processes measured by explicit memory tasks and the neural mechanisms underlying priming effects, respectively. Voss, Lucas, and Paller review electrophysiological, fMRI, and behavioral evidence and build a very strong case that implicit memory can influence measures thought to reflect the explicit process of familiarity. Specifically, they conclude that the ERP FN400 component reflects conceptual implicit memory. This position is in direct opposition to the widely held view that the FN400 reflects familiarity (see Herzmann et al., this issue), which highlights that the nature of this ERP component is currently a hotly debated topic. Nine peer commentaries on this review paper, with a rejoinder by the authors, are also included in this special issue by the following investigators: (1) Howard Eichenbaum, (2) Jason Taylor and Richard Henson, (3) Anne Cleary, (4) Jennifer Ryan, (5) Wei-chun Wang and Andrew Yonelinas, (6) Ilana Dew and Roberto Cabeza, (7) Craig Stark, (8) Scott Hayes and Mieke Verfaellie, and (9) Edward Wilding. In the second review paper, Gotts, Chow, and Martin review electrophysiological, fMRI, and neural modeling evidence to evaluate four proposals of repetition priming: facilitation, sharpening, enhanced neural synchronization, and Bayesian "explaining away". These investigators convincingly argue that repetition priming effects are mediated, to some degree, through enhanced neural synchronization, and outline several experiments that should be able to adjudicate between these proposals of repetition priming. Nine peer commentaries on this review paper, with a rejoinder by the authors, are also included in this special issue by the following investigators: (1) Karl Friston, (2) Michael Ewbank and Richard Henson, (3) Richard Henson, (4) Maximilian Riesenhuber, (5) Kevin Weiner and Kalanit Grill-Spector, (6) David McMahon, (7) Aidan Horner, (8) Gagan Wig, and (9) Ben Dyson and Claude Alain.

All of the empirical papers and review papers in this special issue represent the cutting edge of cognitive neuroscience research and theory on memory. Rather than relying on widespread beliefs and simplistic assumptions, these papers embrace complex cognitive and neural processes to make significant progress toward understanding the spatial-temporal mechanisms of memory. As such, this special issue will provide a framework for future studies that aim to investigate the true neural mechanisms underlying long-term memory.

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