Neuroimaging of Priming: New Perspectives on Implicit and Explicit Memory

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Abstract

Priming refers to a change in the ability to identify or produce an item as a consequence of a specific prior encounter. Priming has been studied extensively in cognitive studies of healthy volunteers, neuropsychological investigations of brain-damaged patients, and, more recently, studies using modern functional neuroimaging techniques such as positron emission tomography and functional magnetic resonance imaging. We review recent neuroimaging studies that have converged upon the conclusion that priming is reliably accompanied by decreased activity in a variety of brain regions. The establishment of this cortical signature of priming is beginning to generate new hypotheses concerning the relation between priming and explicit retrieval, which we illustrate by considering recent experiments on within- and cross-modality priming.

Keywords

priming; amnesia; neuroimaging; implicit memory; explicit memory

Memory is not a unitary or monolithic entity, but instead can be subdivided into distinct forms or systems (Squire, 1992; Tulving & Schacter, 1990). Psychologists have paid considerable attention to a form of memory that is familiar to people from everyday life: explicit or episodic memory, which involves thinking back in time and consciously bringing to mind past experiences. But during the past two decades, researchers have focused increasingly on a largely nonconscious or implicit form of memory, commonly referred to as *priming*, that is less familiar to people on the basis of everyday experience. Priming involves a change in the ability to identify an object or generate a word as a consequence of a specific prior encounter with it, and often occurs outside of awareness (Tulving & Schacter, 1990). In a typical priming experiment, subjects first study a list of target items—words, pictures, and the like—and later perform a task that requires them to identify, produce, or make a decision about studied and nonstudied items. For example, participants might be asked to identify a briefly flashed picture of a piano or a chair, or to produce a word in response to a three-letter stem. Priming occurs when accuracy or speed of task performance is influenced significantly by prior study.

Priming has been the object of intensive empirical and theoretical attention because it can be clearly dissociated from explicit, conscious recollection (Schacter & Buckner, 1998; Wiggs & Martin, 1998). Some of the most dramatic evidence that suggests that priming can occur without explicit recollection comes from studies of brain-injured amnesic patients with damage to the hippocampus and related structures in the inner parts of the temporal lobe (Squire, 1992). Such patients exhibit little or no conscious memory for recent experiences, yet often show normal priming for recently studied words and objects.

Studies of amnesic patients have been critically important because they show that priming does not require the temporal lobe structures that are damaged in these patients and are necessary for explicit remembering. But studies of amnesic patients cannot tell us what parts of the brain are involved in priming. One promising approach to this latter issue makes use of modern functional neuroimaging techniques: positron emission tomography (PET) and functional magnetic resonance imaging (fMRI). PET measures changes in blood flow within regions of the brain, and fMRI measures changes in the amount of oxygen in the blood (the blood's oxygenation level reflects changes in blood flow and volume). Because changes in neural activity are associated with changes in these blood properties, and because both PET and fMRI allow relatively precise localization of such changes, functional neuroimaging provides a useful window on normal human brain function. With respect to priming, PET and fMRI allow examination of brain areas that are more or less activated during performance of tasks on which priming occurs.

NEUROIMAGING OF PRIMING AND EXPLICIT RETRIEVAL: DECREASES AND INCREASES IN BRAIN ACTIVITY

Neuroimaging studies of priming are best considered in the context of related imaging studies of explicit memory (also referred to as explicit retrieval). Such studies have revealed that a variety of brain regions show increased activity when people are given tests that require them to think back to a study episode and recall or recognize previously encountered target items. Virtually all neuroimaging studies of explicit retrieval have revealed increased activity in the anterior (front) parts of the prefrontal cortex (e.g., Tulving, Kapur, Craik, Moscovitch, & Houle, 1994). Although the prefrontal cortex has long been linked with high-level, or "executive," cognitive processes and with aspects of memory, relatively little was known about the function of anterior prefrontal regions until recently. Some imaging studies have also provided evidence of increased activity in the hippocampus and related inner temporal lobe structures during explicit retrieval, but the effects have been less consistent than in prefrontal cortex (see Schacter & Wagner, 1999).

In contrast to the evidence of increased brain activity during explicit retrieval, neuroimaging studies of priming have consistently revealed evidence of decreased activity (decreases have also been observed in studies of explicit retrieval, but almost always accompanied by increases). Participants are scanned while they carry out a task, such as completing three-letter word stems with the first word that comes to mind after studying a list of familiar words. During primed scans, participants are given stems of words that appeared previously in the study list; during unprimed scans, the target items did not appear previously.

Studies using such procedures consistently report decreased activity in several cortical regions during primed scans compared with unprimed scans, but decreases have been especially consistent in a part of the visual cortex (extrastriate area) that is known to be involved in perceptual processing and in specific areas of the frontal lobe that are involved in semantic or conceptual processing (for reviews, see Schacter & Buckner, 1998; Wiggs & Martin, 1998). It is noteworthy that neither of these brain regions is typically damaged in amnesic patients. This could help to explain why amnesic patients often show intact priming effects.

It has been suggested (Schacter & Buckner, 1998; Wiggs & Martin, 1998) that priming-related decreases in brain activity may be related to *repetition suppression*, a phenomenon established in studies of nonhuman primates (for review and discussion, see Desimone & Duncan, 1995). For instance, in a series of studies by Desimone and Miller and their colleagues (summarized in Desimone & Duncan, 1995), animals viewed complex visual objects, such as patterns or faces, while experimenters recorded the activity of cells in the lower, or inferior, temporal (IT) lobe. Repeated exposure to the same stimulus resulted in reduced responses across a substantial proportion of IT cells. Repetition suppression in nonhuman primates and priming-related decreases in humans could reflect the operation of common underlying mechanisms.

Although neuroscientists are far from understanding the exact nature of these neural mechanisms, the establishment of a signature of priming in the form of decreased activity is beginning to suggest new hypotheses concerning the basis of priming and its contribution to different aspects of memory. To illustrate the kinds of new directions and possibilities suggested by the imaging data, we now turn to a recent line of research that uses previous findings as a basis for examining possible interactions between priming and explicit memory.

PRIMING WITHIN AND ACROSS MODALITIES: CONTRIBUTIONS OF EXPLICIT RETRIEVAL

Cognitive studies have shown that priming effects on a number of tasks are larger when target materials are studied and tested in the same sensory modality (e.g., visual-visual or auditory-auditory) than when targets are studied and tested in different sensory modalities (e.g., visual-auditory or auditory-visual). However, on most tasks, some priming still occurs across sensory modalities. Within-modality priming possibly reflects the operation of perceptual memory processes or systems (Tulving & Schacter, 1990). Cross-modality priming, in contrast, cannot depend on purely perceptual processes. Some studies of word priming suggest that it depends on phonological processes involved in word production; cross-modality priming occurs when changes in these processes transfer across modalities (e.g., Kirsner, Dunn, & Standen, 1989).

Other data raise the possibility that explicit or conscious memory processes are more involved in cross- than in within-modality priming. In a study by Jacoby, Toth, and Yonelinas (1993), college students studied words presented either visually or auditorily, and then were tested visually with three-letter word stems. In one condition, the students were instructed to try to complete each stem with a word they recalled from the study phase. In another condition, they were instructed to complete the stems with words that had not been presented during study (in this condition, completing the stem with a studied item—contrary to the experimenter's instruction—indicated implicit or nonconscious retrieval of the item). The data suggested that within-

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modality priming involves implicit retrieval, whereas cross-modality priming involves explicit recollection. In contrast to these results from college students, experiments with amnesic patients reveal intact cross-modality priming on the stem-completion test (for a review, see Badgaiyan, Schacter, & Alpert, 1999).

Taken together, the foregoing results are puzzling: Evidence from college students indicates a role for explicit retrieval in cross-modality priming, whereas evidence from amnesic patients indicates explicit retrieval is not necessary for cross-modality priming to occur. Recent PET studies from our laboratory may help to illuminate the apparent conflict (Schacter, Badgaiyan, & Alpert, 1999; see also Badgaiyan et al., 1999). Participants studied common words either visually or auditorily before scanning was initiated. During scanning, three-letter word beginnings were presented visually, and the participants were asked to complete each stem with the first word that came to mind. In the primed scans, the three-letter stems could be completed with words from the immediately preceding study list; in the unprimed scans, stems could not be completed with words from the study list.

The behavioral data revealed evidence of priming: Subjects produced significantly more studied words during primed than unprimed scans. As in previous studies of visual stem-completion priming, PET data in the within-modality condition revealed decreased activity in regions of visual (extrastriate) cortex during primed compared with unprimed scans. Further, there was no evidence of increased activity during within-modality priming. Results from the cross-modality condition were more complex. There was decreased activity (compared with unprimed scans) during cross-modality priming in the upper part of the left temporal lobe (left superior temporal gyrus), extending into the lower and back part of the parietal lobe. There is experimental evidence that this region is involved in storing and retrieving phonological features of words (for discussion, see Badgaiyan et al., 1999). Accordingly, the involvement of this region in priming across sensory modalities fits with previous proposals that cross-modality priming depends on changes in phonological processing (Kirsner et al., 1989). In addition, however, cross-modality priming was accompanied by increased activity in anterior portions of the prefrontal cortex—regions that are thought to be involved in aspects of explicit retrieval (e.g., Tulving et al., 1994).

When we examined priming on an auditory stem-completion test within and across sensory modalities, we again found that cross-modality priming (visual-to-auditory) was associated with increased activity in anterior prefrontal cortex, and also with decreased activity in the left temporo-parietal region. Within-modality auditory priming was associated only with decreased activity in several different brain regions (see Badgaiyan et al., 1999).

The finding that activity in anterior prefrontal cortex increases during cross- but not within-modality priming, together with findings suggesting these regions play a role in explicit retrieval, supports the suggestion of Jacoby et al. (1993) that explicit retrieval plays a role in cross-modality priming, but not within-modality priming. Why, then, do amnesic patients show normal cross-modality priming in the stem-completion task? Recall that in both of our cross-modality priming experiments, increases in anterior prefrontal activity were accompanied by decreases in left temporo-parietal activity that may signal changes in phonological processing. Amnesic patients typically do not have phonological processing deficits, nor do they have damage to the left temporo-parietal region. We suggest that there are two "routes" to cross-modality priming: one that involves changes in phonological processing and is available to both amnesic patients and healthy persons, and another that involves explicit retrieval and is available only to the latter group. If one of these routes can substitute for the other, then amnesic patients can show intact cross-modality priming based on a preserved phonological route.

Though this hypothesis is somewhat speculative, it does predict that patients with damage to both phonological processing and explicit retrieval should show impaired cross-modality priming in the stem-completion task, because both routes to priming are compromised. Evidence consistent with this idea has been reported recently (Curran, Schacter, & Galluccio, 1999): Patients with phonological deficits and poor explicit memory demonstrated normal within-modality priming and impaired cross-modality priming on a visual stem-completion task.

CONCLUDING COMMENTS

We have reviewed neuroimaging evidence indicating that priming effects within a sensory modality are reliably accompanied by decreases in cortical activity, and provided one example of how these findings may broaden understanding of the contributions of explicit retrieval to cross-modality priming. Several questions remain to be resolved, however. First, priming-related decreases in cortical activity may indicate that brain regions that are involved in initial processing of a word or picture show a kind of "neural savings" when the entire item, or parts of it, is repeated. An alternative possibility is that decreased blood flow is a by-product of the reduced time that participants spend processing primed compared with unprimed items. If participants disengage attention earlier from a primed than a nonprimed test item, decreased blood flow will be observed.

Second, although we have emphasized that within-modality priming is accompanied by decreased cortical activity, increases are sporadically reported. Why? Priming-related decreases occur in studies that use well-learned stimulus materials, such as common words or familiar objects. In contrast, one study that revealed increased cortical activity during within-modality priming used unfamiliar stimulus materials (line drawings of novel geometric shapes; Schacter et al., 1995). Results of a recent fMRI study are consistent with these findings: Henson, Shallice, and Dolan (2000) found that priming-related decreases occurred when participants were exposed to well-learned materials (familiar faces or meaningful symbols), whereas priming-related increases occurred for novel materials (unfamiliar faces or meaningless symbols). Further studies are necessary to assess the generality and theoretical significance of this pattern.

Third, an important question concerns exactly what type of explicit retrieval influences cross-modality priming. In this regard, two aspects of explicit retrieval need to be considered. First, explicit retrieval involves intentional retrieval: the deliberate attempt to think back to a past episode. In the context of a word-stem-completion experiment, intentional retrieval occurs when participants see a word stem (e.g., "tab__") and think back to the study list in an effort to retrieve an appropriate target word. Second, explicit retrieval involves conscious awareness that a retrieved item was presented during an earlier episode. For instance, when given the word stem "tab___," participants might complete it with the first word that comes to mind (*table*), and then become aware that "table" appeared earlier on the study list.

Richardson-Klavehn and Gardiner (1996) showed that intentional retrieval does not play a critical role in cross-modality priming on the stem-completion test; that is, participants do not deliberately attempt to recall words from the study list when given a three-letter word stem. Instead, cross-modality priming involves conscious awareness that completed words appeared earlier in the target list. The observed activations in prefrontal cortex during cross-modality priming suggest that subjects spontaneously became aware that some of their word completions had appeared earlier on the study list. Understanding why such "involuntary explicit memory" occurs for cross-modality priming, but not for within-modality priming, is an important topic for future studies using both cognitive and neuroimaging techniques.

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Acknowledgments—This work was supported by Grant MH57915 from the National Institute of Mental Health and Grant NS27950 from the National Institute of Neurological Disorders and Stroke.

Note

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