Priming and the Brain

Review

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Introduction

Research in cognitive psychology, neuropsychology, and neuroscience has converged recently on the idea that memory is composed of dissociable forms and systems (Squire, 1992; Roediger and McDermott, 1993; Schacter and Tulving, 1994; Willingham, 1997). This conclusion has been based on experimental and theoretical analyses of a variety of different phenomena of learning and memory. One of the most intensively studied of such phenomena is known as *priming*: a change in the ability to identify or produce an item as a result of a specific prior encounter with the item (Tulving and Schacter, 1990).

Priming represents an example of what is often referred to as implicit memory (Graf and Schacter, 1985; Schacter, 1987; Roediger, 1990) or nondeclarative memory (Squire, 1992)—a nonconscious influence of past experience on current performance or behavior. Priming and related types of implicit memory had been noted occasionally since the nineteenth century in clinical and experimental reports but have only been studied systematically during the past two decades (for a historical review, see Schacter, 1987). Modern interest in priming was stimulated by several developments: studies concerning lexical access and representation that provided methods for assessing priming (e.g., Scarborough et al., 1977), early theoretical attempts to distinguish among different forms of memory (e.g., Tulving, 1972), and reports of preserved learning in patients with amnesic syndromes (e.g., Milner et al., 1968; Warrington and Weiskrantz, 1974; see below for discussion). Based on these developments, a number of experiments reported during the early 1980's helped to characterize the phenomenon of priming and distinguish it from explicit memory (cf. Jacoby and Dallas, 1981; Tulving et al., 1982; Graf et al., 1984).

Priming is assessed with experimental tasks that do not require conscious recollection of particular previous experiences. Such tasks differ from traditional tests of recall and recognition, which tap an explicit or declarative form of memory and require conscious, intentional recollection of recently studied information. Consider, for example, a prototypical experiment in which priming is assessed with a word-stem completion test. In the first phase of the experiment, subjects study a series of words. After a delay that usually ranges from several

minutes to several hours, subjects are given three-letter word stems with multiple possible completions and are asked to complete each stem with the first word that comes to mind (e.g., mot___ for the target word "motel"). Priming occurs when subjects complete the stem with a designated target completion more often for words that had been studied earlier than for words that were not studied previously. In a related kind of experiment, subjects study a list of words and are later given a word identification test, where words are flashed briefly (e.g., for 35 ms) and subjects attempt to identify them. Priming occurs when subjects identify more previously studied words than nonstudied words. Similar kinds of tasks have been developed for examining priming of numerous different types of stimuli, including pseudowords (Keane et al., 1995; Bowers, 1996), familiar and unfamiliar objects (Biederman and Cooper, 1991; Srinivas, 1993; Schacter et al., 1993b), visual patterns (Musen and Squire, 1992), and environmental sounds (Chiu and Schacter, 1995; for extensive reviews, see Roediger and McDermott, 1993; Schacter et al., 1993a).

Cognitive studies of healthy volunteers have provided a great deal of information about the behavioral and psychological properties of priming (for discussion of recent research, see Wiggs and Martin, 1998). For example, it is known from numerous cognitive studies that explicit recall and recognition of recently studied words, objects, or other materials is greatly affected by how those materials are initially encoded during the study phase of an experiment (e.g., Craik and Tulving, 1975). More specifically, when target items are initially encoded in a semantic or elaborative manner (e.g., generating meanings of a word or rating its pleasantness), subsequent explicit recall or recognition is much more accurate than when target items are initially encoded in a nonsemantic or shallow manner (e.g., counting the number of vowels and consonants in a word). In an early study of priming, Jacoby and Dallas (1981) reported that priming effects on a word identification test are no greater after semantic encoding than after nonsemantic encoding—even though recognition accuracy was much higher after the semantic than the nonsemantic encoding task (although some subsequent studies have found small effects of semantic versus nonsemantic encoding manipulations on word identification and similar tasks, they are much smaller than the effects of the same encoding manipulations on explicit memory; for a review and discussion, see Brown and Mitchell, 1994). Other early data established that healthy volunteers can show priming even when they fail to consciously recollect that they have previously studied an item and that priming can persist across days (Tulving et al., 1982); more recent data indicate that priming effects can persist for as long as a year (e.g., Cave, 1997).

Whereas the foregoing studies involved college students, research on priming quickly broadened to include a variety of subject populations. For example, studies comparing elderly adults with young adults have shown that age-related decreases in priming tend to be smaller

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than age-related decreases in explicit recall and recognition (see Mitchell, 1993; La Voie and Light, 1994). Likewise, studies of priming in young children have shown a relative invariance of priming in younger and older children (e.g., from 3–10 years of age), even though explicit memory shows strong developmental trends across the same time period (see Parkin, 1993; Naito and Komatsu, 1993). Studies of patients with various psychopathological conditions, including depression and anxiety, have also revealed robust priming effects (see Mineka and Nugent, 1995).

Cognitive studies have been essential in delineating the basic properties of priming, but to obtain a fuller understanding of the phenomenon it is necessary to understand its neural underpinnings. Here, we review evidence concerning the brain systems that are involved in priming, focusing on studies of patients with neurological damage, and on experiments that have used brain imaging techniques—positron emission tomography (PET) and functional magnetic resonance imaging (fMRI)—to explore the neural correlates of priming in healthy volunteers. We believe that characterizing priming at the level of brain systems provides an important foundation that can inform and guide further explorations of priming at cellular and molecular levels.

Neuropsychology of Priming: Insights from Studies of Brain-Injured Patients

Priming and the Amnesic Syndrome

The amnesic syndrome occurs as a consequence of damage to structures in the medial temporal lobe and diencephalon and is characterized by a severe impairment in the explicit recollection of everyday facts and events, together with preservation of general intelligence (Squire, 1992). The syndrome was first brought to the widespread attention of neuroscientists during the 1950's, when Milner and her colleagues described the famous patient H. M., who developed profound amnesia for recent events following bilateral medial temporal lobe resection for the relief of intractable epilepsy (e.g., Milner et al., 1968). Although it initially appeared that H. M. had no ability to retain new information of any kind, Milner et al. (1968) reported that H. M. could learn new motor skills in a relatively normal manner.

Early interpretations attributed the findings of Milner and colleagues to the uniqueness of motor memory. However, evidence obtained from other amnesic patients soon raised the possibility that preserved memory function in amnesics might extend beyond the domain of motor skill acquisition. In a series of important studies, Warrington and Weiskrantz (1974) reported that amnesic patients sometimes show relatively preserved memory performance when they are given word beginnings as cues for previously studied items. This was a striking finding, because patients demonstrated little explicit recollection of the same items when they were shown an entire word and were required to make an old/new judgment about it. However, in Warrington and Weiskrantz's work, the amnesic patients' performance on the fragment cueing test varied across experiments, sometimes attaining normal levels and sometimes showing impairments. Thus, it was unclear whether Warrington and Weiskrantz had uncovered a form of memory that is fully preserved in amnesic patients or whether fragment cueing performance, like other kinds of memory, is impaired by amnesia.

Studies conducted during the early 1980's clarified these findings by demonstrating that performance on the word-stem completion task depends critically on the instructions given to subjects (these instructions were not systematically examined in the Warrington and Weiskrantz studies). When instructed to complete a stem with the first word that comes to mind, amnesic patients showed a normal priming effect compared to control subjects; but when instructed to produce the correct item from the study list, amnesic patients showed less recall than did controls (Graf et al., 1984). Similar patterns were observed when amnesic patients were given related kinds of priming and recall tasks (Schacter, 1985). Normal priming in amnesic patients has since been observed across a variety of different tasks and conditions (for reviews, see Schacter et al., 1993a; Squire, 1992).

Overall, evidence gathered during the past 15 years supports a distinction between explicit memory, which is impaired in amnesic patients and depends on the medial temporal/diencephalic regions that are damaged in amnesia, and priming, which is preserved in amnesia and does not depend on medial temporal/diencephalic structures. Although the possibility has been raised that word priming effects on word completion and identification tests are not preserved in amnesic patients, appearing to be normal because of methodological problems and limitations of relevant studies (Ostergaard and Jernigan, 1993), experiments that have addressed possible methodological problems still reveal normal priming in amnesia (Hamann et al., 1995). Indeed, recent evidence indicates that priming of word completion and word identification performance can be fully preserved even when a patient is unable to attain above-chance scores on forced-choice tests of explicit recognition memory (Hamann and Squire, 1997a). This kind of finding helps to rule out the possibility that priming in amnesic patients is mediated by residual explicit memory abilities, and instead supports the conclusion that priming is mediated by processes or systems that are not essential for explicit memory and are spared in amnesia.

Varieties of Priming: Data and Theoretical Implications

In considering the generality of the conclusion that priming is preserved in amnesic patients, it is important to note that priming can be fractionated into several different subtypes. One basic distinction is between *perceptual priming* and *conceptual priming*. Perceptual priming is modality specific and does not depend on semantic or elaborative encoding of an item at the time of study, whereas conceptual priming is not modality specific and benefits from semantic encoding (Blaxton, 1989). Priming on a word identification test (where subjects try to identify briefly flashed items) represents a relatively "pure" form of perceptual priming: the priming effect is eliminated by modality change between the study and test phases of the experiment (visual-to-auditory or auditory-to-visual), and does not benefit, or benefits only slightly, from prior semantic encoding of target materials during study compared to nonsemantic encoding (even

though explicit recall and recognition benefit greatly from prior semantic encoding). Priming on word completion tests is largely, but not entirely, perceptually based (i.e., the effect is reduced but not eliminated by modality changes and is sometimes influenced significantly by semantic study processing). Conceptual priming, in contrast, is most clearly observed on the category instance production task, where subjects are given category cues (e.g., "fruit") and produce relevant exemplars (e.g., "orange," "pear"); priming occurs when subjects are biased to produce previously studied category exemplars. Other tasks for investigating conceptual priming include answering general knowledge questions and generating word associations. As we will argue later, it is likely that most priming tasks have some perceptual and conceptual components.

Conclusions about preservation of priming in amnesia are usually based on studies of perceptual priming. In addition to previously mentioned findings of normal word completion priming in amnesics, it has also been found that amnesic patients show normal priming on both visual and auditory word identification tests (e.g., Cermak et al., 1985; Schacter et al., 1994), as well as on a picture naming task (Cave and Squire, 1992; Verfaellie et al., 1996). Several studies have examined conceptual priming in amnesic patients, and they have yielded mixed results: amnesic patients have shown normal priming on the category instance production task and word association tasks (Shimamura and Squire, 1984; Schacter, 1985; Graf et al., 1985; Carlesimo, 1994) but showed impaired priming on a conceptual task that involves answering general knowledge questions (Blaxton, 1992; Vaidya et al., 1996).

One problem in evaluating conceptual priming is that explicit retrieval processes may sometimes play a significant role in conceptual priming tasks. Whereas studies of perceptual priming with healthy volunteers have produced experimental dissociations between priming and explicit memory—dissociations that effectively rule out the possibility that subjects use explicit retrieval on the priming task (cf. Schacter et al., 1989; Jacoby, 1991)—it has proven more difficult to obtain such dissocations with conceptual priming tasks (see Mulligan, 1997). Thus, while preserved conceptual priming in amnesic patients shows that explicit memory need not be involved in such priming effects, impaired conceptual priming in amnesic patients may reflect the fact that conceptual priming in control subjects sometimes depends on explicit retrieval processes, at least when the test involved answering general knowledge questions (see Vaidya et al., 1996).

Similar issues have arisen in studies examining whether amnesic patients show priming for novel information or new associations. In most studies that have reported intact perceptual priming in amnesia, target information has a preexisting memory representation (e.g., familiar words are represented in memory prior to the experiment). Several studies have documented, however, that amnesics can exhibit normal perceptual priming for stimuli that do not have a preexisting memory representation—novel visual patterns (Gabrieli et al., 1990; Musen and Squire, 1992), unfamiliar objects (Schacter et al., 1993b), pseudowords (e.g., "BOAF";

Haist et al., 1991), or orthographically illegal nonwords (e.g., "VXRB"; Keane et al., 1995; Hamann and Squire, 1997b; for a review, see Bowers and Schacter, 1993).

Related studies have sought to determine whether amnesic patients can exhibit priming for new associations between entirely unrelated words. For example, after studying an unrelated word pair (e.g., window–reason), control subjects are more likely to complete the word stem "rea___" with "reason" when the stem is paired with "window" than when it is repaired with another unrelated word from the study list (Graf and Schacter, 1985). Severely amnesic patients typically show impaired priming of new associations on the word completion test (e.g., Schacter and Graf, 1986; Shimamura and Squire, 1989). However, priming of new associations on the word completion test often depends on the encoding and retrieval of both perceptual and conceptual information (Graf and Schacter, 1989; see also Goshen-Gottstein and Moscovitch, 1995). Recent evidence indicates that amnesic patients can show priming of new associations on a word identification test (which depends largely or entirely on the encoding and retrieval of perceptual information) when previously studied word pairs or repaired words are flashed simultaneously and subjects try to identify both words (Gabrieli et al., 1997). This finding raises the possibility that amnesic patients show intact priming of new perceptual associations, but evidence from related tasks is mixed (cf. Moscovitch et al., 1986; Musen and Squire, 1993; Paller and Mayes, 1994). It remains unclear as to whether impaired priming of new associations in amnesic patients indicates that amnesics are unable to form the kinds of novel representations that support some types of implicit retrieval of new associations (Musen and Squire, 1993) or that such priming effects in control subjects sometimes depend on explicit retrieval (Bowers and Schacter, 1990; Reingold and Goshen-Gottstein, 1996).

Similar issues have arisen in studies examining whether amnesic patients exhibit what have come to be known as form-specific priming effects. Studies of healthy volunteers have shown that priming effects can be larger when target items are studied and tested in the identical physical format than when a perceptual feature of the target item is changed between study and test. For example, priming effects on a visual word identification test or a visual word completion test are sometimes greater when words are studied and tested in the same typefont or case (upper versus lower) than when typefont or case is changed between study and test (e.g., Roediger and Blaxton, 1987; Graf and Ryan, 1990; Marsolek et al., 1992, 1996; Wiggs and Martin, 1994; Curran et al., 1996; but see Carr et al., 1989, and Rajaram and Roediger, 1993, for failures to obtain form-specific priming). Similarly, priming effects on auditory word completion and identification tests can be greater when words are studied and tested in the same voice than in a different voice, or even when the fundamental frequency of a single speaker's voice is changed between study and test (Church and Schacter, 1994). Form-specific priming effects have also been observed on tasks involving identification of, or decisions about, pictures of visual objects. For example, in picture identification tasks,

greater priming effects are observed when the same exemplar (e.g., the identical picture of a car) is presented at study and test compared to two different exemplars (e.g., pictures of two different cars; Biederman and Cooper, 1991; Srinivas, 1993); form-specific visual priming has also been observed when objects are rotated between study and test (see Cooper and Schacter, 1992; Srinivas, 1995).

Form-specific priming is potentially important because it indicates that priming can be influenced by novel, highly specific information about the particular features of items presented during the study episode, and because it may also reveal important characteristics of the representations that support priming (for discussion, see Marsolek et al., 1992, 1996; Tenpenny, 1995; Bowers, 1996; Curran et al., 1996). Relevant evidence from amnesic patients is mixed: some studies have failed to find form-specific visual priming (Kinoshita and Wayland, 1993) or auditory priming (Schacter et al., 1995a), whereas other studies have delineated conditions in which amnesic patients can show intact form-specific priming in both visual (Vaidya et al., 1998) and auditory (Schacter and Church, 1995) domains. Although the exact reasons for the different outcomes is not well understood, Schacter and Church (1995) and Vaidya et al. (1998) provide discussions of alternative possibilities.

In summary, the evidence indicates that perceptual priming of both familiar and unfamiliar words, objects, and patterns is generally preserved in amnesic patients, whereas conceptual priming of familiar information, priming of new associations, and form-specific priming are sometimes preserved and sometimes impaired. The findings on preserved perceptual priming in amnesia provide support for the view that this type of priming depends on a brain system that is distinct from the medial temporal/diencephalic system that supports explicit memory. For example, Tulving and Schacter (1990) proposed that priming depends on a perceptual representation system (PRS) involved in processing information about the form and structure, but not the meaning and associative properties, of words and objects. It has been proposed that the PRS contains a number of subsystems dedicated to the representation of visual word forms, auditory word forms, and shapes of objects, and that such subsystems depend on posterior cortical regions (Schacter, 1994). Because such regions are usually not damaged in amnesic patients, it seems likely that perceptual priming depends on these subsystems. While proposals of this kind focus on the brain systems that support priming and explicit memory, they have been complemented by cognitive models that focus on the processing activities that are engaged by different types of tasks. Such models attempt to explain differences between priming and explicit memory in terms of the different forms of processing that are required by implicit and explicit memory tasks (Blaxton, 1989; Roediger and McDermott, 1993). By combining the systems-based view developed on the basis of neuropsychological observations with the process-oriented view developed from cognitive analyses, it is possible to provide a fuller theoretical analysis than either view can supply alone (cf. Roediger, 1990; Schacter, 1992; Gabrieli, 1995; Ratcliff and McKoon, 1997).

Beyond Amnesia: Insights from Dementias and Focal Cortical Lesions

Studies of amnesic patients have provided crucial insights into the relation between priming and the brain. Studies of other kinds of patient populations have begun to yield a number of new insights that extend and complement the data from amnesic patients. For example, amnesic patients exhibit both intact perceptual priming and intact motor skill learning, so it is unclear whether these two phenomena depend on a common neural substrate or whether they depend on different brain systems. To address this question, a number of studies have examined priming in patients with Huntington's disease, who are characterized by damage to the basal ganglia and exhibit severe deficits in motor skill learning. However, patients with Huntington's disease show intact perceptual priming on tasks such as word completion and identification (for a review, see Salmon and Butters, 1995), thereby suggesting that perceptual priming and motor skill learning depend on different brain systems.

The relation between perceptual priming and semantic processing has been illuminated by evidence from patients with focal cortical lesions. Schacter et al. (1993c) examined perceptual priming in a patient, J. P., who had suffered a stroke in the left medial/inferior temporal gyrus that produced a rare condition known as *word meaning deafness*: J. P. had great difficulty comprehending spoken words, even though he could repeat those words (indicating relatively intact auditory perception), and could also perceive and understand written words. Schacter et al. found that J. P. showed normal perceptual priming on an auditory word identification test (in which previously studied and nonstudied words were masked by white noise), even though he exhibited severely impaired auditory comprehension of the target words. Geva et al. (1997) examined priming in a patient (N. G.) with a focal cortical (left temporal) lesion who is characterized by another relatively rare syndrome known as *prosopanomia*—a specific impairment in the retrieval of proper names. Though N. G. had great difficulty spontaneously retrieving the names of persons and cities, after exposure to person and city names N. G. showed a normal perceptual priming effect on a word-fragment completion test. Geva et al. suggested that priming in patient N. G. is supported by intact perceptual representations, whereas the patient's name retrieval deficit results from a problem in retrieving the phonology of the name from a semantic representation.

Studies of patients with focal lesions to posterior cortical areas, together with studies of patients with Alzheimer's disease, are helping to clarify the relationship between perceptual and conceptual priming. Like amnesic patients, Alzheimer's patients are characterized by severe deficits in explicit recall and recognition, which are produced by pathology (i.e., neuritic plaques and neurofibrillary tangles) in the hippocampal formation (for a recent review, see Boller and Duyckaerts, 1997). In addition, however, Alzheimer's patients are also characterized by pathology to frontal and temporal neocortical regions, together with relative sparing of occipital cortex (Arnold et al., 1991). Several studies have shown that Alzheimer's patients exhibit normal perceptual

priming on the word identification test but show impaired conceptual priming on the category instance production test (Keane et al., 1991, 1994; Monti et al., 1996; cf. Maki and Knopman, 1996). Alzheimer's patients have also shown intact perceptual priming of novel visual patterns on a task that requires completion of partial patterns (Postle et al., 1996). In contrast, priming on the word-stem completion test is often, but not always, impaired in patients with Alzheimer's disease (see Monti et al., 1996), perhaps reflecting a conceptual component to stem-completion priming. The conceptual priming impairment is likely attributable to pathology in anterior neocortical regions that are spared in amnesia.

In contrast, the opposite pattern of findings has been reported in patients with focal damage to occipital cortex. For example, Gabrieli et al. (1995) described a patient, M. S., who had most of his right occipital lobe removed for relief of intractable epilepsy. M. S. fails to show perceptual priming on a word identification test but shows normal conceptual priming on a category instance production test (see also Carlesimo et al., 1994, for similar observations of a related patient). Combined with the results from studies of amnesic patients and patients with Alzheimer's disease, these findings provide evidence for a double dissociation between perceptual and conceptual priming. These kinds of results also illustrate how studies of different types of patient populations can provide complementary evidence concerning the brain regions that are involved in priming. Studies of amnesic patients provide strong evidence that medial temporal/diencephalic structures are *not* necessary for perceptual priming but do not provide evidence concerning which structures *are* involved in such priming effects. Studies of patients with focal occipital lesions help to complete the puzzle by showing that regions of occipital cortex do play a role in perceptual (but not conceptual) priming. Additional converging evidence concerning the brain regions that are relevant to priming has been provided by recent neuroimaging studies.

Priming and Neuroimaging

During the past several years, there has been a sharp increase in studies using two major neuroimaging techniques to investigate memory encoding and retrieval processes: positron emission tomography (PET), which measures changes in regional cerebral blood flow, and functional magnetic resonance imaging (fMRI), which measures changes in blood oxygenation level associated with changes in blood flow and volume (for reviews, see Ungerleider, 1995; Cabeza and Nyberg, 1997; Buckner and Koutstaal, 1998). Because changes in net neural activity are associated with changes in these blood properties (Raichle, 1987), functional neuroimaging provides a unique window through which to view normal human brain function. With respect to priming, PET and fMRI allow examination of brain areas that are activated during performance of tasks for which priming effects are observed, and they also permit investigation of how activation levels change when items are primed. We will first consider studies that have focused on perceptual components of priming. We will then summarize studies

that have focused on conceptual components of priming and also consider evidence bearing on the interrelations between the two components of priming.

Neuroimaging of Perceptual Priming

The first neuroimaging studies of perceptual priming were reported by Squire and colleagues (Squire et al., 1992; Buckner et al., 1995). Subjects studied words prior to PET scans; during a series of scans several minutes later, they were asked to complete the stems to form the first words that came to mind. Behavioral data revealed evidence of priming: stems of previously studied words were completed more often with target items than were novel stems, and subjects took less time to produce the studied words in comparison to completion of novel stems. PET blood flow data indicated that bilateral posterior perceptual processing areas in extrastriate occipital cortex (which were activated during completion of novel stems) showed reduced activation when word stems were primed. Such an effect may reflect a neural correlate of perceptual priming: after exposure to a stimulus, subsequent processing is faster and requires less neural activity (for converging evidence from research using event-related potentials [ERPs], see Badgaiyan and Posner, 1997).

Interpretation of these early findings was complicated by the additional finding that, in the study of Squire et al. (1992), priming was associated with a small but significant blood flow increase in the vicinity of the hippocampal formation (right parahippocampal gyrus). The hippocampal activation may have reflected the fact that subjects had studied the target words twice under semantic encoding conditions that promote high levels of explicit memory. Consistent with the idea that the hippocampal activation was not directly related to perceptual priming, subsequent research has shown that when explicit memory is greatly reduced by the use of a nonsemantic encoding task that produces poor explicit memory, the priming-related hippocampal activation reported by Squire et al. is eliminated, whereas the priming-related blood flow reduction in extrastriate cortex is still observed (Schacter et al., 1996). After considering these and related findings at length, Schacter and Buckner (1998) concluded that the hippocampal activation observed by Squire et al. during perceptual priming may reflect an involuntary "contamination" of priming performance by explicit retrieval (for further relevant evidence, see Rugg et al., 1997).

Importantly, PET findings of blood flow reductions in posterior cortical regions during perceptual priming have been extended to several other priming tasks using fMRI. Studies in which priming was assessed with such tasks as visual word-stem completion, visual word-fragment completion, generation of verbs to visually presented nouns, and classification of objects all show reductions in posterior cortical regions when repeated items are compared to novel items (Martin et al., 1995, Soc. Neurosci., abstract; Blaxton et al., 1996; Buckner et al., 1997; for a review and discussion, see Buckner and Koutstaal, 1998; Schacter and Buckner, 1998).

In a recent study (Buckner et al., 1998 [this issue of *Neuron*]), we examined priming using newly developed procedures for analyzing event-related fMRI. One limitation of previous PET and fMRI studies is that items from

different experimental conditions had to be presented in separate "blocks," in contrast to the usual practice in cognitive studies of intermixing items from different conditions. With respect to priming, presenting old and new items in separate blocks could allow subjects to change strategies or allocate attention differently to old and new items. By contrast, when using event-related fMRI procedures, different types of stimuli can be intermixed randomly, and responses to the novel and repeated items can be separated and analyzed in an event-locked manner, similar to how ERPs and single-unit physiologic data are handled (Dale and Buckner, 1997, Josephs et al., 1997; for a review of event-related fMRI procedures see Rosen et al., 1998).

In our event-related fMRI study of priming, subjects were instructed to classify colored pictures of objects as tending either to move (e.g., a car) or to stay still (e.g., a tree). Priming was revealed by the finding that subjects were faster to make decisions about repeated objects as compared to novel objects. By rapidly presenting the trials in randomly intermixed format, subjects could not have anticipated or adjusted strategies for novel or repeated items to produce such an effect; the behavioral facilitation was produced entirely by the prior history (i.e., novel versus repeated) of the individual item. Analysis of fMRI data indicated robust activation reductions in posterior cortical areas when comparing the repeated and novel objects. Moreover, examination of the anatomic locations of the reductions indicated that higher-level visual areas were most affected, whereas early visual areas falling at or near striate cortex were least affected, thereby suggesting that the priming-related decreases show anatomic specificity. This finding is consistent with a study that examined the anatomic specificity of visual word priming-related reductions in relation to visual area boundaries defined by retinotopic organization (Halgren et al., 1997). In the study of Halgren et al., robust activation reductions were noted in late visual areas with little or no reductions noted in early visual areas, as defined by retinotopy.

Neuroimaging of Conceptual Priming:
Relations to Perceptual Priming

The foregoing findings are generally consistent with the idea that priming can be attributable, at least in part, to facilitation of perceptual processes. Several studies have also examined conceptual priming effects on tasks that require semantic processing (for direct comparisons between conceptual and perceptual priming and recall tasks, see Blaxton et al., 1996). More specifically, such studies have documented that robust and consistent reductions can be detected in higher-order prefrontal brain regions when words are repeated across verbal processing tasks requiring semantic elaboration. For example, Raichle et al. (1994) observed that generating verbs that are meaningfully related to presented nouns could be facilitated by repeated exposure to the nouns. After many repetitions, robust blood flow reductions were noted in left prefrontal cortex. Demb et al. (1995) presented subjects with words and asked them to classify each word as abstract or concrete. Similar to the Raichle et al. study, left prefrontal regions showed reduced activation during performance with repeated items compared to novel items, even after a single item

exposure. Wagner et al. (1997b) and Buckner et al. (1998) recently reported similar prefrontal reductions for repeated semantic classification of object pictures. Importantly, the left prefrontal regions that showed activation reductions during conceptual priming have also shown activation increases during semantic encoding tasks relative to perceptual encoding tasks (e.g., Kapur et al., 1994; Demb et al., 1995; Gabrieli et al., 1996; Buckner and Koutstaal, 1998; for relevant evidence from patients with lesions of left inferior frontal cortex, see Swick and Knight, 1996). Considered along with the previously discussed findings concerning perceptual priming, the overall pattern of data raises the possibility that activation reductions in posterior (i.e., extrastriate) cortical regions are specifically associated with perceptual priming, whereas activation reductions in left prefrontal regions are specifically associated with conceptual priming (see Figure 1). Though such an interpretation is appealing in its simplicity, this view is no doubt oversimplistic because it does not take into account important differences in task parameters between studies. To illustrate the point, consider studies that used word-stem completion to investigate perceptual priming and decisions about whether words are abstract or concrete to investigate conceptual priming. In prior studies of word-stem completion (Squire et al., 1992; Buckner et al., 1995; Schacter et al., 1996), subjects engaged in an orienting task during study (e.g., they made semantic or perceptual judgments about the target words); they did not engage in a word-stem completion task. Thus, the same items were repeated (at least partially) from the study list to the word-stem test, but the task itself differed at study and test. By contrast, in the studies by Raichle et al. (1994) and Demb et al. (1995) that showed priming-related prefrontal reductions, the identical tasks were performed across item repetitions. This observation raises two questions: (1) would prefrontal reductions be diminished or eliminated when items are initially presented under different task conditions than at test, even for the same tasks that have shown robust prefrontal reduction when repeated exactly (e.g., Demb et al., 1995); and (2) would tasks such as word-stem completion, which typically show priming effects in across-task conditions, show priming-related prefrontal reductions when the exact task is repeated? In a series of fMRI studies (Buckner et al., 1997; Koutstaal et al., 1997; Wagner et al., 1997a; for a discussion see Buckner and Koutstaal, 1998, and Schacter and Buckner, 1998), our group has provided evidence bearing on each of these questions.

In one experiment, subjects performed word-stem completion with a repeating set of stem cues during particular fMRI task blocks and with novel word-stem cues during other blocks. Contrasting the novel with the repeated blocks, fMRI data showed reduced activation for repeated word-stems in left dorsal and inferior prefrontal regions (Buckner et al., 1997; Koutstaal et al., 1997). A parallel design was used for a verb generation task that has been linked previously with prefrontal reductions (Raichle et al., 1994), and similar results were obtained. Thus, contrary to the possibility that word-stem completion is associated only with blood flow

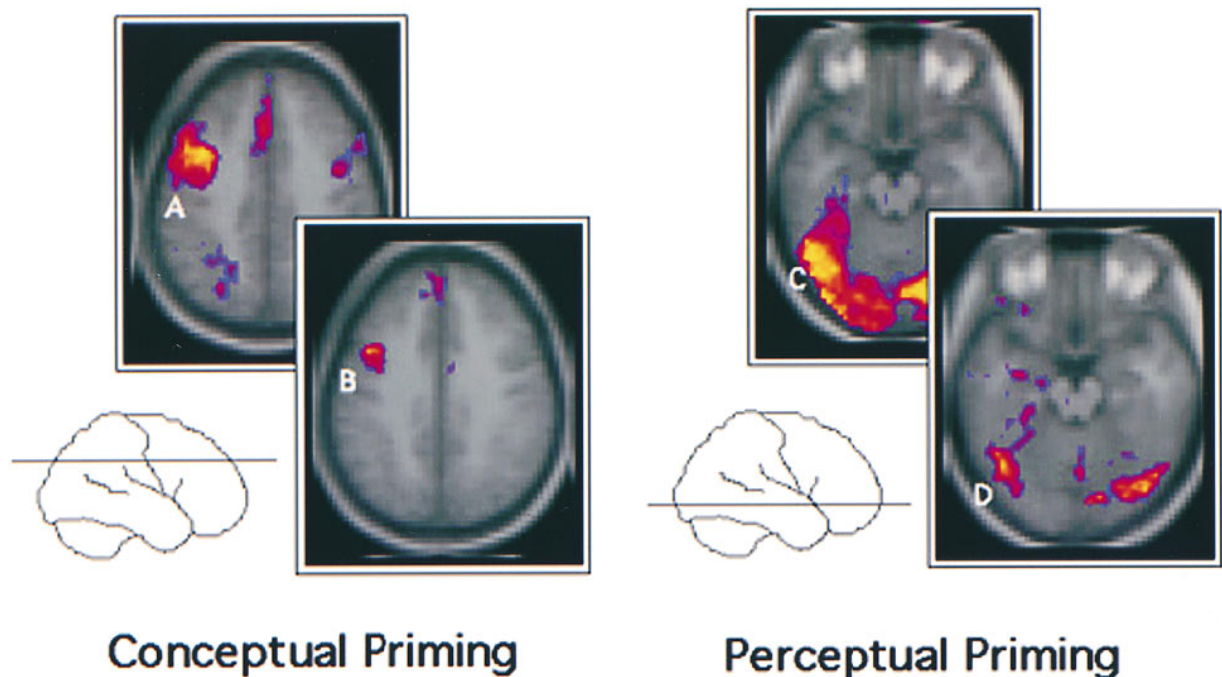## Conceptual Priming

Perceptual Priming

Figure 1. Activation Reductions Associated with Perceptual and Conceptual Priming

Activation reductions have been observed frequently across a number of studies in which item repetition yields priming (e.g., Squire et al., 1992; Raichle et al., 1994; Demb et al., 1995; Buckner et al., 1995, 1997, 1998; Schacter et al., 1996; see text for discussion). This phenomenon is illustrated above in two sets of fMRI images from our laboratory. Each set shows one activation image (upper left) where novel items are compared to a low level reference task, revealing all areas activated by the task. The second activation image (bottom right) shows the direct comparison between the novel and repeated items, revealing those areas in which activation levels are reduced as a consequence of priming. Left prefrontal areas that activate for novel items (A) have, in many instances, shown reductions in activation (B), perhaps as a reflection of conceptual priming. An area in extrastriate visual cortex that is activated by presentation of novel visual words (C) reduces activation to repeated visual words (D). Reductions in visual cortex activity may underlie perceptual priming. Not all areas activated by a task show priming-related reductions, as can be observed in the comparison between (C) and (D): certain areas activated in (C) do not show reductions in (D). As noted in the text, the areas showing reductions are anatomically selective. The color scale in the images represents the significance of the activation, with brighter colors indicating increased significance. The schematic of the brain on the left shows the approximate level from which the section is taken.

reductions in brain regions that perform perceptual analyses, the overall patterns of blood flow reductions indicate that word-stem completion (like verb generation or word categorization) is neither an entirely perceptually driven task nor an entirely conceptually driven task. Rather, item and task overlap determines which kinds of processes will be engaged at study and test and, therefore, which will manifest priming-related modulations. Note that findings of left prefrontal reductions during word-stem completion performance converge with recent neuropsychological evidence from studies of elderly adults showing a correlation between the magnitude of stem-completion priming and performance on neuropsychological tasks sensitive to frontal lobe dysfunction (Winocur et al., 1996).

Evidence bearing on this latter point has been provided in studies by Wagner et al. (1997a), based on previous work by Demb et al. (1995), in which items were repeated across two tasks: one involved a perceptual decision and the other involved a conceptual decision. Demb et al. (1995) reported that when items were repeated across the perceptual decision task, there were no activation reductions in left prefrontal cortex. However, the perceptual decision task likely did not activate

left prefrontal cortex initially, so it is difficult to interpret the lack of activation reduction across trials. Wagner et al. (1997a) used a paradigm in which words were presented initially during the perceptual decision task and were tested again on the conceptual (abstract/concrete) decision task. This manipulation revealed that (1) left dorsal prefrontal cortex was activated by the abstract/concrete decision task and (2) the activation was not reduced as a consequence of prior exposure to the items in the perceptual decision task. By contrast, in a second condition using the abstract/concrete decision task, where the exact items and task demands were repeated over several trials, across-trial reductions in left prefrontal activity were noted, as initially reported by Demb et al. (1995).

Considered together, all of the foregoing findings converge to suggest one neural correlate of priming: repeating items during performance of the same task, or even during performance of different tasks, can lead to decreases in the amount of activation present in specific brain areas. The reductions appear to be selective, depending on item and task overlap across repetitions; they are also characterized by anatomic specificity, with higher-level visual areas showing greater reductions

than earlier visual areas (Figure 1). Overall, the neuro-imaging data converge with the previously reported results of studies with patient populations: the regions that consistently show priming-related blood flow reductions are not usually damaged in amnesic patients, and one region that has consistently shown blood flow reductions during perceptual priming—extrastriate visual cortex—is selectively damaged in a patient who shows impaired perceptual priming (Gabrieli et al., 1995). To link the results from neuropsychological populations and neuroimaging more tightly, it will be necessary to use neuroimaging techniques to examine priming in relevant patient populations. Although little data are yet available, Buckner and Koutstaal (1998) provide preliminary fMRI data indicating that conceptual priming in amnesia is accompanied by left prefrontal activation reductions, as previously observed in normal subjects (Demb et al., 1995).

One open question is how functional changes revealed after a single repetition of an item—the procedure used most often in studies of priming—will relate to paradigms in which items are repeated numerous times. On the one hand, both kinds of procedures have revealed similar activation reductions in specific brain areas. For example, the previously mentioned studies by Raichle et al. (1994) and Demb et al. (1995) reveal qualitatively similar reductions in prefrontal areas even though Raichle et al. examined task performance after numerous exposures, whereas Demb et al. characterized changes after a single repetition. On the other hand, extensive repetition has been associated with changes beyond those described here in relation to priming. For example, Raichle et al. (1994) noted increases in activation in bilateral insular cortex following extensive repetition. They hypothesized that with extensive exposure to items, alternative functional anatomy is utilized—perhaps reflecting the transition from a brain pathway underlying a more effortful mode of task performance with novel items, to one driven by automatic response selection for items that have been repeated extensively. Although priming-related increases in activation have occasionally been observed in single repetition experiments (e.g., Schacter et al., 1995b), priming-related decreases are far more common in such studies. Thus, further research is needed to clarify how functional changes observed during the early stages of item repetition, which we tend to describe in terms of priming, are related to later stages such as those observed by Raichle et al., which may be more akin to what has traditionally been termed skill learning (see Ungerleider, 1995, for initial discussion of this issue).

Concluding Comments

Progress in understanding the relation between priming and the brain has been facilitated greatly by the interplay between cognitive studies of individuals with intact memory functions, neuropsychological investigations of patients with memory disorders, and functional neuroimaging research. It seems likely that the interplay among these different approaches will continue to deepen our understanding of priming.

One notable gap in current approaches concerns the absence of a well-developed animal model of priming. However, recent studies using single-unit recording techniques in nonhuman primates have begun to fill the gap and to illuminate possible mechanisms of priming. For example, in studies by Desimone and Miller and their colleagues (summarized by Desimone et al., 1995; see also Ringo, 1996), animals fixated on a series of complex visual objects, such as patterns or faces, while the activity of populations of cells in inferior temporal (IT) cortex was recorded. Repeated exposure to the same stimulus yielded reduced responses in a substantial proportion of IT cells; the reduced responding persisted across as many as 150 intervening items. The effect could not be attributed to generalized habituation, because introduction of novel stimuli produced a return to initial levels of activity. These findings bear a striking resemblance to the previously discussed priming-related activation reductions observed in neuroimaging studies with humans (see Desimone, 1996). Wiggs and Martin (1998) have pointed out a number of additional similarities between phenomena of "repetition suppression" (Desimone et al., 1995) observed in animals and priming phenomena. Although we cannot be certain that repetition suppression effects are based on the same processes that underlie perceptual priming in humans, the similarities between the two types of phenomena are suggestive enough to merit careful study in future investigations. The development of an animal model of priming could help to lay the foundations for an eventual understanding of priming at cellular and even molecular levels of analysis. Such a development would greatly extend the systems-level analyses that have proven so useful in the cognitive neuroscience investigations that have helped to uncover and illuminate the phenomenon of priming.

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