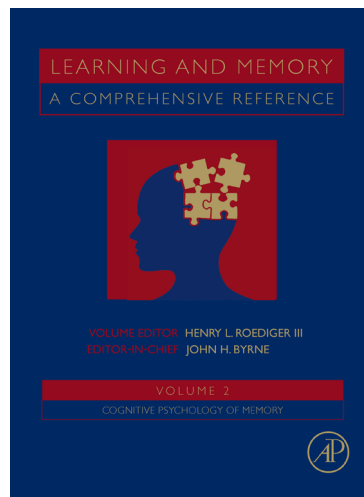


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2.33 Implicit Memory and Priming

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2.33.1 Introduction

Priming refers to an improvement or change in the identification, production, or classification of a stimulus as a result of a prior encounter with the same or a related stimulus (Tulving and Schacter, 1990). Cognitive and neuropsychological evidence indicates that priming reflects the operation of implicit or nonconscious processes that can be dissociated from those that support explicit or conscious recollection of past experiences. More recently, neuroimaging studies have revealed that priming is often accompanied by decreased activity in a variety of brain regions (for review, see Schacter and Buckner, 1998; Wiggs and Martin, 1998; Henson, 2003), although conditions exist in which priming-related increases are also observed (e.g., Schacter et al., 1995; Henson et al., 2000; Fiebach et al., 2005). Various terms have been used to describe these neural changes, including adaptation, mnemonic filtering, repetition suppression, and repetition enhancement. These terms often refer to subtly distinct, though related, phenomena, and in some cases belie a theoretical bias as to the nature of such neural changes. Thus, throughout the present review, the term neural priming will be used to refer to changes in neural activity associated with the processing of a

stimulus that result from a previous encounter with the same or a related stimulus.

When considering the link between behavioral and neural priming, it is important to acknowledge that functional neuroimaging relies on a number of underlying assumptions. First, changes in information processing result in changes in neural activity within brain regions subserving these processing operations. A second assumption underlying positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) is that these changes in neural activity are accompanied by changes in blood flow, such that the energy expenditure that accompanies increased neuronal processing elicits the delivery of metabolites and removal of by-products to and from active regions, respectively. It is these local vascular changes that are measured: PET measures changes in cerebral blood flow and oxygen or glucose utilization, while fMRI measures the ratio of oxygenated to deoxygenated hemoglobin (i.e., the blood-oxygen-level dependent, or BOLD, signal). Related techniques such as event-related potentials (ERP) and magnetoencephalography (MEG), by contrast, measure the electrophysiological responses of neural populations more directly, although at a cost of decreased spatial resolution. While this chapter will focus on fMRI and to a lesser extent PET

studies of priming, ERP and MEG studies will be discussed when they are of special interest to the discussion of a particular topic.

Neuroimaging studies have provided new means of addressing cognitive theories that have traditionally been evaluated through behavioral studies. The primary goal of the present chapter is to examine how neuroimaging evidence has informed, influenced, and reshaped cognitive theories about the nature of priming. We focus on five research areas where such interaction has occurred: influences of explicit versus implicit memory, top-down attentional effects, specificity of priming, the nature of priming-related activation increases, and correlations between brain activity and behavior.

2.33.2 Influences of Explicit Versus Implicit Memory

Priming is typically defined as a nonconscious or implicit form of memory. This characterization is supported by numerous observations of spared priming in amnesic patients with severe disorders of explicit memory. However, starting with the earliest cognitive studies of priming in healthy volunteers, researchers have been concerned with the possibility that subjects may use some type of explicit retrieval to perform a nominally implicit task. This concern has led to the development of various cognitive procedures for estimating and removing the influences of explicit retrieval (e.g., Schacter et al., 1989; Jacoby, 1991). Two forms of such explicit ‘contamination’ have received attention in cognitive studies: (1) subjects realize that their memory is being tested, and intentionally retrieve study list words while performing a priming task to augment performance; (2) subjects follow task instructions, and therefore do not engage in intentional retrieval, but nonetheless unintentionally recollect that they had studied target items on the previous study list. With respect to the latter type of contamination, it has been noted that explicit memory often takes the form of unintentional or involuntary recollections of previous experiences in which there is no deliberate, effortful attempt to think back to the past; one is spontaneously ‘reminded’ of a past event that is accompanied by conscious recollection (e.g., Schacter, 1987; Schacter et al., 1989; Richardson-Klavehn et al., 1994; Richardson-Klavehn and Gardiner, 1998; Bernsten and Hall, 2004). We now consider findings from neuroimaging studies that

provide insights into the nature of and relation between implicit and explicit influences on priming.

The explicit contamination issue arose in the first neuroimaging study of priming (Squire et al., 1992). In this experiment, subjects semantically encoded a list of familiar words prior to PET scanning and were then scanned during a stem completion task in which they provided the first word that came to mind in response to visual three-letter word stems. During one scan, subjects could complete stems with study list words (priming), and during another, they could complete stems only with new words that had not been presented on the study list (baseline). In a separate scan, subjects were provided with three-letter stems of study-list words, and were asked to think back to the study list (explicit cued recall).

Priming was associated with decreased activity in the right extrastriate occipital cortex compared with baseline, but there was also increased activity in the right hippocampal formation during priming compared with the baseline condition. In light of previous results from amnesic patients indicating that normal stem-completion priming can occur even when the hippocampal formation is damaged, it seemed likely that the observed activation of the hippocampal region reflects one of the two previously mentioned forms of ‘contamination’: subjects intentionally retrieved words from the study list or, alternatively, they provided the first word that comes to mind and involuntarily recollected its prior occurrence.

Schacter et al. (1996) attempted to reduce or eliminate explicit influences by using a nonsemantic study task (counting the number of t-junctions in each of target words), which in previous behavioral studies had supported robust stem-completion priming together with poor explicit memory for the target items (e.g., Graf and Mandler, 1984; Bowers and Schacter, 1990). Consistent with the idea that the priming-related hippocampal activation previously observed by Squire et al. reflects contamination from explicit memory that is not essential to observing priming, following the t-junction encoding task there was no evidence of priming-related increases in the vicinity of the hippocampal formation during stem completion performance relative to the baseline task, but there were priming-related decreases in bilateral extrastriate occipital cortex and several other regions.

Using PET, Rugg et al. (1997) found greater left hippocampal activity after deep encoding than after shallow encoding during both intentional (old/new

recognition) and unintentional (animate/inanimate decision) retrieval tasks. They also observed greater right anterior prefrontal activity during intentional retrieval than during unintentional retrieval after both deep and shallow encoding. These results suggest that increases in hippocampal activity during explicit retrieval, unaccompanied by corresponding increases in anterior prefrontal activity, reflect the presence of involuntary explicit memory.

A more recent event-related fMRI study by Schott et al. (2005) extends the findings of these early studies. During the study phase, subjects made nonsemantic encoding judgments in which they counted the number of syllables in each word. During the test phase, Schott et al. used a stem completion task and directly compared performance during intentional retrieval (i.e., try to remember a word from the list beginning with these three letters) and incidental retrieval (i.e., complete the stem with the first word that comes to mind). Importantly, they used a behavioral procedure developed by Richardson-Klavehn and Gardiner (1996, 1998) in which participants indicate whether or not they remember that the item they produced on the completion task had appeared earlier during the study task. This procedure could be applied to both the incidental and intentional tests, because on the intentional test subjects were told to complete stems even when they could not recall a study-list item. In the scanner, subjects used a button press to indicate whether they had covertly completed a stem; between these test trials, they provided their completions orally and indicated whether or not they remembered having seen the item during the study task. Stems completed with study-list words that were judged as nonstudied were classified as primed items, whereas stems completed with study-list words judged as studied were classified as remembered items. Both primed and remembered items were compared with baseline items that subjects judged correctly as nonstudied.

Similar to previous studies, Schott et al. (2005) documented activation reductions for primed items compared with baseline items in a number of regions, including extrastriate visual cortex. However, because the primed items in this study were, by definition, ones that subjects did not consciously remember having encountered previously, these data show more convincingly than earlier studies that priming-related activation decreases can reflect strictly nonconscious or implicit memory. Moreover, the authors also reported that their findings

concerning priming-related reductions during the incidental tests were largely replicated during the intentional test. Thus, the results support the idea that priming effects can occur during both intentional and unintentional retrieval. Several other regions, including the right prefrontal cortex, showed greater activity during the intentional than the incidental task. In contrast to prior studies, the hippocampus showed greater activity during baseline than during priming, which the authors attributed to novelty encoding. Overall, these neuroimaging results support earlier behavioral distinctions between strategic controlled retrieval (i.e., intentional vs. incidental) and conscious recollection of the occurrence of previously studied items and show clearly that priming-accompanied activation reductions can occur without conscious recollection.

While the foregoing studies attempted to distinguish implicit and explicit aspects of priming by focusing on retrieval, other studies have done so by examining brain activity during encoding. Schott et al. (2006) examined subsequent memory effects, where neural activity during encoding is sorted according to whether items are subsequently remembered or forgotten (e.g., Brewer et al., 1998; Wagner et al., 1998). This study reported fMRI data from the encoding phase of the aforementioned stem completion experiment reported by Schott et al. (2005), where participants counted the number of syllables in each word. Consistent with results from earlier subsequent memory studies that examined explicit retrieval, Schott et al. found greater activation during encoding for subsequently remembered than for forgotten items in left inferior prefrontal cortex and bilateral medial temporal lobe. By contrast, encoding activity in these areas was not associated with subsequently primed items. Instead, subsequent priming was associated with activation decreases during encoding in bilateral extrastriate cortex, left fusiform gyrus, and bilateral inferior frontal gyrus. These regions were distinct from those that showed priming-related decreases during the stem completion test. Schott et al. suggest that their data indicate that priming, in contrast to explicit memory, is associated with sharpening of perceptual representations during encoding, an idea that is consistent with previous theories emphasizing the differential role of a perceptual representation system in priming and explicit memory (Schacter, 1990, 1994; Tulving and Schacter, 1990).

While the combined results from Schott et al.'s (2005, 2006) encoding and retrieval phases highlight

clear differences between priming and explicit memory, a related study by Turk-Browne et al. (2006), also using a subsequent memory paradigm, uncovered conditions under which the two forms of memory are associated with one another. Subjects made indoor/outdoor decisions about a series of novel scenes. Each scene was repeated once, at lags ranging from 2 to 11 items. Fifteen minutes after presentation of the final scene, subjects were given a surprise old/new recognition test. Turk-Browne et al. focused on a region of interest in the parahippocampal place area (PPA) that responds maximally to visual scenes (e.g., Epstein and Kanwisher, 1998). The critical outcome was that repeated scenes produced behavioral priming and reduced activation in the PPA, but only for those scenes that were subsequently remembered. Forgotten items did not produce either behavioral or neural priming. A whole-brain analysis revealed similar effects – neural priming for remembered items only – in bilateral PPA as well as in left inferior temporal gyrus and bilateral angular gyrus. However, forgotten items were associated with neural priming in the anterior cingulate.

Given the general trend that behavioral and neural priming both depended on subsequent explicit memory, Turk-Browne et al. suggested that their data reveal a link between implicit and explicit memory that involves some aspect of shared encoding processes – most likely that selective attention during encoding is required for both subsequent priming and explicit memory.

The neuroimaging evidence considered thus far reveals some conditions under which priming can occur independently of explicit memory and others where dependence exists. An experiment by Wagner et al. (2000) showed that priming can sometimes hinder explicit memory. They made use of the well-known spacing or lag effect, where reencoding an item after a short lag following its initial presentation typically produces lower levels of subsequent explicit memory than reencoding an item after a long lag (though in both cases, explicit memory is higher than with no repetition). Using an incidental encoding task (abstract/concrete judgment) and old/new recognition task, Wagner et al. documented greater explicit memory following a long- than a short-lag condition, consistent with previous behavioral findings. By contrast, they showed greater behavioral priming, indexed by reduced reaction time, and greater neural priming, indexed by reduced activity in the left inferior frontal lobe, following a

short lag than a long lag. Moreover, there was a negative correlation between the magnitude of neural priming in the left inferior frontal region and the level of subsequent explicit memory. Thus, the short-lag condition that maximized priming also reduced explicit memory. Although the exact mechanism underlying the effect is still not known, Wagner et al. suggested that priming may impair new episodic encoding and later explicit memory by reducing encoding variability, that is, encoding different attributes of repeated items on different trials. To the extent that encoding variability normally enhances subsequent memory by providing multiple retrieval routes to an item (e.g., Martin, 1968), priming might reduce explicit memory because it biases encoding toward sampling the same item features on multiple trials. Whatever the ultimate explanation, these results highlight the role of a previously unsuspected interaction between priming and explicit memory in producing a well-known behavioral effect.

2.33.3 Top-Down Attentional Effects on Priming

Priming is often considered to be an automatic process (e.g., Jacoby and Dallas, 1981; Tulving and Schacter, 1990; Wiggs and Martin, 1998). However, recent neuroimaging evidence has revealed that, to some extent, behavioral and neural priming may be affected by top-down cognitive processes such as attention or task orientation.

2.33.3.1 Priming: Automatic/Independent of Attention?

Early evidence supported the notion that perceptual priming effects occur independent of manipulations of attention (for review see Mulligan and Hartman, 1996). However, subsequent findings from behavioral studies began to reveal that some perceptual priming effects do depend to some degree on attention at study (e.g., Mulligan and Hornstein, 2000).

In a seminal review that linked behavioral priming with the phenomenon of repetition suppression, Wiggs and Martin (1998) stated that this process “happens automatically in the cortex” and “is an intrinsic property of cortical neurons,” and that “perceptual priming is impervious to ... attentional manipulations” (Wiggs and Martin, 1998: 231). Indeed, there is some compelling evidence from studies with monkeys

to suggest that repetition-related neural priming can occur independent of attention (e.g., Miller et al., 1991; Miller and Desimone, 1993; Vogels et al., 1995), but these findings do not speak directly to neural priming in humans. Some neuroimaging evidence shows that conditions exist under which both behavioral and neural priming are unaffected by manipulations of attention. A PET study by Badgaiyan et al. (2001) investigated the effects of an attentional manipulation during the study phase of a cross-modal priming task. Target words were aurally presented among distracter words at study under either full attention or under a divided-attention task. At test, visual word stems were presented in separate blocks for both target word types. Behavioral priming (faster reaction times) and neural priming (reduced regional cerebral blood flow in superior temporal gyrus) were of similar magnitude for words presented under full and divided attention conditions (see also Voss and Paller, 2006).

An fMRI study that we reviewed earlier (Schott et al., 2005) further demonstrated that changing the nature of the task to be performed during the test phase did not affect the level of behavioral or neural priming. Following shallow encoding of words at study, word stems were presented in separate blocks of either an implicit or an explicit memory task at test. Although the explicit task elicited a higher rate of explicit recollection of previously studied words, there were no differences in behavioral priming effects between the two conditions – i.e., subjects produced an equivalent number of previously studied words when cued with word stems in both test conditions. Moreover, an equivalent degree of neural priming was documented in left fusiform, bilateral frontal, and occipital brain regions in both implicit and explicit conditions. Thus, this experiment demonstrated that changing the task orientation at test had no effect on behavioral or neural priming.

Hasson et al. (2006) demonstrated comparable neural priming in some brain regions despite a change of task orientation across separate sessions (i.e., separate experiments with different tasks). In the first of two experiments, subjects listened to spoken sentences, some grammatically sensible, some nonsensible, and decided whether each sentence was sensible or not. In the second experiment, subjects passively listened to spoken sensible sentences only, making no judgments or responses. A direct contrast between the two tasks indicated that neural priming in temporal regions was equivalent across conditions. However, neural priming was also

observed in inferior frontal regions, but only in the active condition in which subjects made sensible/nonsensible judgments. This finding suggests that attentional manipulations have variable effects on different brain regions.

The foregoing studies have demonstrated that behavioral and/or neural priming can occur independent of shifts in attentional demands or task orientation at study (Badgaiyan et al., 2001; Voss and Paller, 2006), at test (Schott et al., 2005), or between different tasks (Hasson et al., 2006). However, consistent with the latter finding by Hasson et al. of concurrent attenuation of priming in prefrontal regions associated with changing task demands, these null results do not rule out the possibility that under different task conditions, and in different brain regions, top-down attentional effects may play an important role in priming. We consider now (and also later in the chapter) recent evidence that supports this claim.

2.33.3.2 Priming: Modulated by Attention

Henson et al. (2002) reported one of the first neuroimaging studies to demonstrate that neural priming is modulated by top-down cognitive factors. Subjects viewed pictures of famous and nonfamous faces, each presented twice at random intervals within one of two separate, consecutive task sessions. During the implicit task session, subjects performed a continuous famous/nonfamous face discrimination task; during the explicit task session, subjects performed a continuous new/old face recognition task. Neural priming was observed in a face-responsive region in the right fusiform gyrus for repeated famous faces only, consistent with previous findings (Henson et al., 2000), as well as for both famous and nonfamous faces in a left inferior occipital region. Neural priming in these regions occurred only in the implicit task. As stimuli were identical across the different task conditions, the modulation of neural priming was attributed to top-down effects of task orientation.

Although there were effects of attention on neural priming, behavioral priming seemed to be unaffected by top-down factors. Rather, behavioral priming, as indexed by reduced reaction time to respond to repeated presentations of famous faces relative to initial presentations, was equivalent in the implicit and explicit tasks. This result implies a dissociation between behavioral priming and neural priming observed in these brain regions. Further, attentional modulation varied only between sessions, i.e., the

same task was performed on each stimulus during the initial and repeated presentations, leaving open the question of whether attentional factors exert an influence at study, at test, or on both occasions.

A subsequent fMRI study tested the hypothesis that attentional factors, specifically at study, have an impact on neural priming (Eger et al., 2004). During fMRI scanning, subjects performed a task at study in which two objects were simultaneously presented, one to the left and one to the right of a central fixation point. Importantly, subjects were cued to attend to either the left or right of center by a visual cue presented onscreen 100 ms prior to presentation of the 'prime' stimuli. A single 'probe' stimulus was subsequently presented in the center of the screen that matched the previously attended stimulus, matched the previously unattended stimulus, was the mirror image of one of these two stimuli, or was novel. Analyses of repetition-related behavioral facilitation (faster reaction times) and neural response reductions (fMRI BOLD signal decreases in fusiform and lateral occipital regions) revealed that behavioral and neural priming occurred only for probes that matched (or mirrored) the attended prime. Conversely, no behavioral or neural priming was documented when the probe stimulus matched (or mirrored) the unattended prime. Thus, this study showed that modulation of spatial attention affects behavioral as well as neural priming in object selective perceptual processing regions, and that these top-down attentional effects exert an influence specifically at the time of study.

In a face-repetition priming study, Ishai et al. (2004) reported that neural priming occurred only for repeated faces that were task relevant. Subjects were presented with a target face and then were shown a series of faces, including three repetitions of the target face, three repetitions of a nontarget face, and seven distracter faces. Participants were required to push a button each time the target face appeared, and thus were required to attend to all faces, although only the target face was task relevant. Significant neural priming (reduced BOLD response for the third relative to the first repetition) was observed in face-responsive regions, including inferior occipital gyri, lateral fusiform gyri, superior temporal sulci, and amygdala, but only for the target face repetitions; no neural priming was associated with repetition of nontarget faces.

Yi and colleagues (Yi and Chun, 2005; Yi et al., 2006) used overlapping scene and face images to also demonstrate that task-relevant attention has an effect

even for simultaneously viewed stimuli. In one experiment, participants were presented with overlapping face and scene images and instructed to attend only to the face or the scene on a given trial (Yi et al., 2006). Neural priming in a face-responsive fusiform region was documented only for repeated faces that were attended, and not for scenes or unattended faces. Similarly, neural priming in a scene-responsive parahippocampal region occurred only for repeated scenes that were attended, and not for faces or unattended scenes. Surprisingly, even after sixteen repetitions of a stimulus every 2 s within a block, no trace of neural priming was observed for unattended stimuli in these respective regions (Yi et al., 2006).

Thus, while a number of neuroimaging studies have shown that both behavioral and neural priming can remain constant across study and test manipulations of attention or between different tasks with common stimuli, several studies reviewed here indicate that top-down effects of attention can have an impact on behavioral and/or neural priming, both at the time of study (Henson et al., 2002) and at test (Ishai et al., 2004), and have been shown to involve both spatial attention (Eger et al., 2004) and task-relevant selective attention (Ishai et al., 2004; Yi and Chun, 2005; Yi et al., 2006). To reconcile these ostensibly incongruent conclusions requires a more detailed consideration of the nature of subtle differences in various manipulations of attention, and importantly, of the particular brain regions involved.

Accordingly, recent studies (e.g., Hassan et al., 2006) have begun to dissociate various brain regions that are differentially sensitive to various attentional manipulations. In a study by Vuilleumier et al. (2005), participants viewed overlapping objects drawn in two different colors at study and were instructed to attend only to objects of a specified color. At test, these objects were presented singly among novel real and nonsense objects, and subjects indicated whether each object was a real or nonsense object. Behavioral priming was documented both for previously attended and ignored objects, with a relative boost in performance for objects that were attended. However, different brain regions showed differential sensitivity to the effects of attention on neural priming. A group of regions that comprised right posterior fusiform, lateral occipital, and left inferior frontal regions demonstrated neural priming only for attended objects presented in the original view. By contrast, bilateral anterior fusiform regions were insensitive to changes of viewpoint (original vs.

mirrored), but showed neural priming for unattended objects in addition to more robust neural priming for attended objects. Finally, neural priming in the striate cortex was view specific and more robust for attended than ignored objects.

In keeping with the latter findings, O'Kane et al. (2005) reported a similar dissociation between brain regions differentially sensitive to manipulation of top-down processes. Subjects were presented with words at study and performed a judgment of either size, shape, or composition in separate task blocks. At test, subjects performed a size judgment for all studied words presented among novel words. Behavioral facilitation, as measured by faster reaction times for size judgments at test, was observed for repeated relative to novel words, with an additional benefit when the judgment was the same at study and test (size/size) relative to when the judgment was switched (shape/size or composition/size). Neural priming in left parahippocampal cortex tracked the behavioral trend, showing reduced BOLD responses for repeated relative to novel words, with an additional trend toward increased priming when the task was the same across repetition. In left perirhinal cortex, however, neural priming occurred for repeated words only when the judgment was the same at study and test. The finding that perirhinal cortex is sensitive to semantic but not perceptual repetition provides evidence that this region is involved in conceptual processing.

Considered together, the neuroimaging studies reviewed here suggest that behavioral and neural priming are indeed modulated by top-down cognitive factors of attention or task orientation, but that this modulation exerts differential effects across different brain regions depending on the nature of the task. Neural priming within a given brain region may occur only to the extent that the processing of a stimulus reengages this region in a qualitatively similar manner across repetitions.

2.33.3.3 Neural Mechanisms of Top-Down Attentional Modulation

Although the effects of attention on priming have now been well documented, little is known about the neural mechanisms that underlie these top-down effects. Efforts to understand these mechanisms have been at the forefront of recently emerging neuroimaging research.

Increased attention at the time of study has been suggested as an important factor in priming.

Turk-Browne et al. (2006), as previously reviewed in this chapter, reported that neural priming occurred only for repeated scenes that were later remembered, but not for those scenes that were later forgotten. They found that tonic activation, a general measure of regional neural activity, was elevated for scenes that were later remembered and that also elicited neural priming upon repeated presentation. While previous evidence indicates that increased attention results in increased neural firing rates within process-relevant brain regions, a recent fMRI study suggests that attention may also increase selectivity of the neural population representing an attended stimulus (Murray and Wojciulik, 2004).

Other neuroimaging approaches, including MEG and EEG, have been used to further characterize the nature of attentional modulations of neural priming as well. Evidence supporting the hypothesis that attention serves to increase specificity of perceptual representations was reported by Duzel and colleagues (2005) in a study using MEG. By investigating neural activity at study, they compared words that showed subsequent behavioral priming (faster reaction times) to those that did not show subsequent priming. They reported relatively decreased amplitude, but increased phase alignment, of beta and gamma oscillations for words that showed later priming, indicating increased specificity of the neural response for these words at the time of study. Further, they reported increased coordination of activity between perceptual and higher brain regions for words that showed subsequent priming, as measured by increased interareal phase synchrony of alpha oscillations. Importantly, this increased synchrony between perceptual and higher brain regions was detected immediately prior to the initial presentation of the subsequently primed stimuli, indicating an anticipatory effect. These results suggest that top-down processes, through anticipatory coordination with perceptual brain regions, increase specificity of perceptual representations at study. Such a process may also be necessary at test for successful priming. Gruber et al. (2006) reported that 'sharpening' of the neural response in cell assemblies (as measured by suppression of induced gamma band responses in ERPs) occurred for repeated visual stimuli only when the task was the same at both study and test, but not when the task was switched.

Therefore, through a combination of various neuroimaging techniques, researchers have begun to characterize the neural mechanisms that underlie attentional modulation of priming. These

mechanisms may constitute a link between the cognitive functions that are accessible to our conscious awareness and under our volitional control and the unconscious systems that facilitate fluency of mental processing.

2.33.4 Specificity of Priming

Priming effects vary in their specificity, that is, the degree to which priming is disrupted by changes between the encoding and test phases of an experiment. When study/test changes along a particular dimension produce a reduction in priming, the inference is that the observed priming effect is based to some extent on retention of the specific information that was changed; when level of priming is unaffected by a study/test change, the inference is that priming reflects the influence of an abstract representation, at least with respect to the changed attribute. Questions concerning the specificity of priming have been prominent since the early days of priming research in cognitive psychology, when evidence emerged that some priming effects are reduced when study/test sensory modality is changed (e.g., [Jacoby and Dallas, 1981](#); [Clarke and Morton, 1983](#)) and can also exhibit within-modality perceptual specificity, shown by the effects of changing typeface or case for visual words (e.g., [Roediger and Blaxton, 1987](#); [Graf and Ryan, 1990](#)), or speaker's voice for auditory words (e.g., [Schacter and Church, 1992](#)). Considerable theoretical debate has focused on the key issue raised by studies of specificity effects, namely whether priming reflects the influence of nonspecific, abstract preexisting representations or specific representations that reflect perceptual details of an encoding episode (for review and discussion of cognitive studies, see [Roediger, 1990](#); [Schacter, 1990, 1994](#); [Roediger and McDermott, 1993](#); [Tenpenny, 1995](#); [Bowers, 2000](#)).

Considering the early cognitive research together with more recent neuropsychological and neuroimaging studies, [Schacter et al. \(2004\)](#) recently proposed a distinction among three types of specificity effects: stimulus, associative, and response. Stimulus specificity occurs when priming is reduced by changing physical properties of a stimulus between study and test; associative specificity occurs when priming is reduced because associations between target items are changed between study and test; and response specificity occurs when priming is reduced because subjects make different responses to the same stimulus

item at study and test. We will review here evidence from neuroimaging studies concerning each of the three types of priming specificity and consider how the imaging data bear on the kinds of theoretical questions that have been of interest to cognitive psychologists.

2.33.4.1 Stimulus Specificity

Most neuroimaging research has focused on stimulus specificity, which is observed by changing physical features of a stimulus between study and test. As mentioned earlier, cognitive studies have shown that priming effects are sometimes modality specific, that is, reduced when study and test sensory modalities are different compared with when they are the same. Such effects are most commonly observed on tasks such as word or object identification, stem completion, or fragment completion, which require perceptual or data-driven processing ([Roediger and Blaxton, 1987](#)). Amnesic patients have shown a normal modality-specific effect in stem completion priming (e.g., [Carlesimo, 1994](#); [Graf et al., 1985](#)), suggesting that this effect is not dependent on the medial temporal lobe structures that are typically damaged in amnesics.

Early neuroimaging studies of within-modality visual priming that compared brain activity during primed and unprimed stem completion showed that priming is associated with decreased activity in various posterior and prefrontal cortical regions, but the decreases were observed most consistently in the right occipitotemporal extrastriate cortex (e.g., [Squire et al., 1992](#); [Buckner et al., 1995](#); [Schacter et al., 1996](#)). These and related findings raised the possibility that priming-related reductions in extrastriate activity are based on a modality-specific visual representation, perhaps reflecting tuning or sharpening of primed visual word representations ([Wiggs and Martin, 1998](#)). Consistent with this possibility, [Schacter et al. \(1999\)](#) directly compared within-modality visual priming to a cross-modality priming condition in which subjects heard words before receiving a visual stem completion task. They found priming-related reductions in extrastriate activity during within- but not cross-modality priming. Surprisingly, however, other neuroimaging studies of within-modality auditory stem completion priming also revealed priming-related activity reductions near the extrastriate region that was previously implicated in visual priming ([Badgaiyan et al., 1999](#); [Buckner et al., 2000](#); [Carlesimo et al., 2004](#)). These results remain poorly understood, but it has been

suggested that one part of the extrastriate region (V3A, within BA 19) is involved in multimodal functions, perhaps converting perceptual information from one modality to another (Badgaiyan et al., 1999).

Although the results of imaging studies comparing within- and cross-modality priming are not entirely conclusive, studies of within-modality changes in physical properties of target stimuli have provided clear evidence for stimulus-specific neural priming, which in turn implicates perceptual brain mechanisms in the observed priming effects. Studies focusing on early visual areas have provided one source of such evidence. Grill-Spector et al. (1999) found that activation reductions in early visual areas such as posterior lateral occipital complex (LOC) exhibit a high degree of stimulus specificity for changes in viewpoint, illumination, size, and position. By contrast, later and more anterior aspects of LOC exhibit greater invariance across changes in size and position relative to illumination and viewpoint. Evidence from a study by Vuilleumier et al. (2005) considered in the previous section likewise indicates a high degree of stimulus specificity in early visual areas, as indicated by viewpoint-specific neural priming in these regions.

Later visual regions can also show stimulus-specific neural priming, but several studies indicate that this specificity effect is lateralized. In a study by Koutstaal et al. (2001), subjects judged whether pictures of common objects were larger than a 13-inch-square box, and later made the same judgments for identical objects, different exemplars of objects with the same name, and new objects. Behavioral priming, indicated by faster response times, occurred for both identical objects and different exemplars, with significantly greater priming for identical objects. Reductions in activation were also greater for same than for different exemplars in the bilateral middle occipital, parahippocampal, and fusiform cortices. These stimulus-specific activation reductions for object priming were greater in the right than in the left fusiform cortex. Simons et al. (2003) replicated these results and further demonstrated that left fusiform cortex shows more neural priming for different exemplars compared with novel items relative to right fusiform cortex, indicating more nonspecific neural priming in the left fusiform. Also, left but not right fusiform neural priming was influenced by a lexical-semantic manipulation (objects were accompanied by presentation of their names or by nonsense syllables), consistent with a lateralized effect in which right fusiform is modulated by specific physical

features of target stimuli and left fusiform is influenced more strongly by semantic features. In a related study by Vuilleumier et al. (2002), subjects decided whether pictorial images depicted real or nonsense objects, and subsequently repeated stimuli were identical, differed in size or viewpoint, or were different exemplars with the same name. Neural priming in the right fusiform cortex was sensitive to changes in both exemplar and viewpoint.

A similar pattern has also been reported for orientation-specific object priming by Vuillemer et al. (2005) in the overlapping shape paradigm described earlier, and Eger et al. (2005) reported a stimulus-specific laterality effect using faces. In the latter experiment, subjects made male/female judgments about famous or unfamiliar faces that were preceded by the identical face, a different view of the same face, or an entirely different face. Behavioral priming, indexed by decreased response times, was greater for same than different viewpoints for both famous and unfamiliar faces. Collapsed across famous and unfamiliar faces, neural priming was more viewpoint dependent in right fusiform gyrus than in left fusiform gyrus. In addition, for famous faces, priming was more nonspecific in anterior than more posterior fusiform cortex. Similarly, Vuillemer et al. (2005) report some evidence for greater stimulus-specific neural priming in posterior compared with anterior fusiform gyrus. Other studies indicate that later perceptual regions can exhibit largely nonspecific priming, both for visual stimuli such as scenes (Blondin and Lepage, 2005) and auditory words (Orfanidou et al., 2006; see also Badgaiyan et al., 2001). However, evidence provided by Bunzeck et al. (2005) suggests that effects in later perceptual regions are characterized by category specificity. In their study, subjects made male/female judgments about faces and indoor/outdoor judgments about scenes. Subjects responded more quickly to repeated faces and scenes compared with initial presentations, thus demonstrating behavioral priming. Face-responsive regions in fusiform and related areas showed selective activation reductions for repeated faces, whereas place-responsive regions in parahippocampal cortex showed decreases for repeated scenes.

By contrast, regions of inferior frontal gyrus and left inferior temporal cortex appear to respond invariantly to an item's perceptual features and are instead sensitive to its abstract or conceptual properties – even when the degree of perceptual overlap between initial and subsequent presentations of a stimulus is minimal to nonexistent. Neural priming has been observed in

these regions during reading of mirror-reversed words initially presented in a normal orientation (Ryan and Schnyer, 2006) and also when silently reading semantically related word pairs, but not for pairs that are semantically unrelated (Wheatley et al., 2005). Consistent with this observation, neural priming in these regions is independent of stimulus modality (Buckner et al., 2000) and has even been observed when the modality differs between the first and second presentations of a stimulus (e.g., visual to auditory; Badgaiyan et al., 2001; Carlesimo et al., 2003).

Overall, then, the foregoing studies reveal a fairly consistent pattern in which neural priming in early visual regions exhibits strong stimulus specificity, whereas in later visual regions, right-lateralized stimulus specificity is consistently observed (for a similar pattern in a study of subliminal word priming, see Dehaene et al., 2001). These effects dovetail nicely with previous behavioral studies using divided-visual-field techniques that indicate that visually specific priming effects occur to a greater extent in the left visual field (right hemisphere) than in the right visual field (left hemisphere) (e.g., Marsolek et al., 1992, 1996).

The overall pattern of results from neuroimaging studies of stimulus specificity suggests that, consistent with a number of earlier cognitive theories (e.g., Roediger, 1990; Schacter, 1990, 1994; Tulving and Schacter, 1990), perceptual brain mechanisms do indeed play a role in certain kinds of priming effects.

2.33.4.2 Associative Specificity

Research concerning the cognitive neuroscience of associative specificity began with studies examining whether amnesic patients can show priming of newly acquired associations between unrelated words. For example, amnesic patients and controls studied pairs of unrelated words (such as window–reason or officer–garden) and then completed stems paired with study list words (window–rea___) or different unrelated words from the study list (officer–rea___). Mildly amnesic patients and control subjects showed more priming when stems were presented with the same words from the study task than with different words, indicating that specific information about the association between the two words had been acquired and influenced priming, but severely amnesic patients failed to show associative priming (Graf and Schacter, 1985; Schacter and Graf, 1986). A number of neuropsychological studies have since

examined associative specificity in amnesics with mixed results (for review, see Schacter et al., 2004), and it has been suggested that medial temporal lobe (MTL) structures play a role in such effects. Some relevant evidence has been provided by a PET study that used a blocked design version of the associative stem completion task (Badgaiyan et al., 2002). Badgaiyan et al. found that, as in previous behavioral studies, priming was greater when stems were paired with the same words as during the study task than when they were paired with different words. The same pairing condition produced greater activation in the right MTL than did the different pairing condition, suggesting that associative specificity on the stem completion task may indeed be associated with aspects of explicit memory. Given the paucity of imaging evidence concerning associative specificity, additional studies will be needed before any strong conclusions can be reached.

2.33.4.3 Response Specificity

While numerous behavioral studies had explored stimulus specificity and associative specificity prior to the advent of neuroimaging studies, the situation is quite different when considering response specificity, where changing the response or decision made by the subject about a particular item influences the magnitude of priming (note that we use the terms ‘response specificity’ and ‘decision specificity’ interchangeably, since behavioral data indicate that the effect is likely not occurring at the level of a motor response; see Schnyer et al., in press). Recent interest in response specificity has developed primarily as a result of findings from neuroimaging research. Dobbins et al. (2004) used an object decision priming task that had been used in studies considered earlier (Koutstaal et al., 2001; Simons et al., 2003), but modified the task so that responses either remained the same or changed across repeated trials. In the first scanning phase, pictures of common objects were either shown once or repeated three times, and subjects indicated whether each stimulus was bigger than a shoebox (using a ‘yes’ or ‘no’ response). Next, the cue was inverted so that subjects now indicated whether each item was ‘smaller than a shoebox’; they made this judgment about new items and a subset of those that had been shown earlier. Finally, the cue was restored to ‘bigger than a shoebox,’ and subjects were tested on new items and the remaining items from the initial phase.

If priming-related reductions in neural activity that are typically produced by this task represent facilitated size processing, attributable to ‘tuning’ of relevant aspects of neural representations, then cue reversal should have little effect on priming (though it could disrupt overall task performance by affecting both new and primed items). According to the neural tuning account, the same representations of object size should be accessed whether the question focuses on ‘bigger’ or ‘smaller’ than a shoebox. By contrast, if subjects perform this task by rapidly recovering prior responses, and this response learning mechanism bypasses the need to recover size representations, then the cue reversal should disrupt priming-related reductions. When the cue is changed, subjects would have to abandon the learned responses and instead reengage the target objects in a controlled manner in order to recover size information.

During the first scanning phase, standard priming-related activation reductions were observed in both anterior and posterior regions previously linked with priming: left prefrontal, fusiform, and extrastriate regions. But when the cue was reversed, these reductions were eliminated in the left fusiform cortex and disrupted in prefrontal cortex; there was a parallel effect on behavioral response times. When the cue was restored to the original format, priming-related reductions returned (again there was a parallel effect on behavioral response times), suggesting that the reductions depended on the ability of subjects to use prior responses during trials. Accordingly, the effect was seen most clearly for items repeated three times before cue reversal.

Although this evidence establishes the existence of response-specific neural and behavioral priming, there must be limitations on the effect, since a variety of priming effects occur when participants make different responses during study and test. For instance, priming effects on the stem completion task, where subjects respond with the first word that comes to mind when cued with a three-letter word beginning, are typically observed after semantic or perceptual encoding tasks that require a different response (see earlier discussion on top-down attentional influences). Nonetheless, the existence of response specificity challenges the view that all activation reductions during priming are attributable to tuning or sharpening of perceptual representations, since such effects should survive a response change. Moreover, these findings also appear to pose problems for theories that explain behavioral priming effects on object decision and related tasks in terms

of changes in perceptual representation systems that are thought to underlie object representation (e.g., Schacter, 1990, 1994; Tulving and Schacter, 1990), since these views make no provisions for response specificity effects. By contrast, the transfer appropriate processing view (e.g., Roediger et al., 1989, 1999) inherently accommodates such effects. According to this perspective, priming effects are maximized when the same processing operations are performed at study and at test. Although this view has emphasized the role of overlapping perceptual operations at study and at test to explain priming effects on tasks such as object decision, to the extent that the subject’s decision or response is an integral part of encoding operations, it makes sense that reinstating such operations at test would maximize priming effects.

However, there is one further feature of the experimental paradigm that Dobbins et al. (2004) used to produce response specificity that complicates any simple interpretation. Priming in cognitive studies is usually based on a single study exposure to a target item, but neuroimaging studies of priming have typically used several study exposures in order to maximize the signal strength. As noted earlier, Dobbins et al. found that response specificity effects were most robust for items presented three times during the initial phase of the experiment (high-primed items), compared with items presented just once (low-primed items).

A more recent neuropsychological investigation of response specificity in amnesic patients highlights the potential theoretical importance of this issue (Schnyer et al., 2006). Schnyer et al. compared amnesics and controls on a variant of the object decision task used by Dobbins et al. (2004). Objects were presented either once (low primed) or thrice (high primed), and then responses either remained the same (‘bigger than a shoebox?’) or were switched (‘smaller than a shoebox?’). Consistent with Dobbins et al. (2004), controls showed greater response specificity for high-primed objects compared with low-primed objects. Amnesic patients showed no evidence of response specificity, demonstrating normal priming for low-primed items and impaired priming for high-primed items. That is, healthy controls showed greater priming for high- than for low-primed objects in the same response condition, but amnesics failed to show this additional decrease in response latencies.

These results raise the possibility that different mechanisms are involved in priming for objects presented once versus those presented multiple times. Perhaps single-exposure priming effects on the object

decision task depend primarily on perceptual systems that operate independently of the MTL and thus are preserved in amnesic patients. In neuroimaging experiments, such effects might reflect tuning or sharpening of perceptual systems, independent of the specific responses or decisions that subjects make regarding the object. But for items presented several times, subjects may learn to associate the object with a particular response, perhaps requiring participation of medial temporal and prefrontal regions. These considerations also suggest that response or decision specificity in the object decision paradigm used by [Dobbins et al. \(2004\)](#) is better described in terms of stimulus-response or stimulus-decision specificity – that is, the formation of a new link between a particular stimulus and the response or decision. This idea is supported by recent behavioral data showing that response-specific priming occurs only for the exact object that was studied, and not for a different exemplar with the same name ([Schnyer et al., in press](#)). In any event, the overall pattern of results suggests that a single-process model is unlikely to explain all aspects of these neural or behavioral priming effects, a point to which we return later in the chapter.

2.33.5 Priming-Related Increases in Neural Activation

Our review so far has focused on behavioral facilitation and corresponding repetition-related reductions of neural activity associated with priming. However, under some conditions, priming has been associated with decrements in stimulus processing, such as slower responses to previously ignored stimuli relative to novel stimuli (i.e., the ‘negative priming’ effect – a term coined by [Tipper, 1985](#)) and poorer episodic encoding for highly primed items ([Wagner, et al., 2000](#)). Further, while repetition-related increases in neural activity have long been associated with explicit memory processes, neural increases associated with priming have also been documented, although less frequently. Neuroimaging studies have begun to investigate the nature of such neural increases and the conditions that elicit them. This research suggests a link between performance decrements and increased neural responses associated with priming and provides new evidence that speaks to competing cognitive theories of implicit memory.

2.33.5.1 Negative Priming

Negative priming (NP) occurs when a stimulus is initially ignored, and subsequent processing of the stimulus is impaired relative to that of novel stimuli. An early example of identity NP was demonstrated by [Tipper \(1985\)](#); overlapping drawings of objects drawn in two different colors were presented, and subjects were instructed to attend to and identify objects of only one specified color. At test, identification of previously presented objects that were ignored was significantly slower than identification of novel objects. The NP effect has since been documented across a diverse range of experimental tasks and stimuli (for review, see [Fox, 1995](#); [May et al., 1995](#)). Efforts to characterize the nature of this processing have sparked a number of theoretical debates within the cognitive psychology literature. One of these debates has centered on the cause of NP (e.g., whether it relies on processes during encoding or later retrieval), while another has focused on determining the level of processing that ignored items undergo in order to elicit NP (e.g., perceptual vs. semantic processing).

Competing accounts of the cause of NP are offered by two theories. The selective inhibition model ([Houghton and Tipper, 1994](#)) proposes that representations of ignored stimuli are initially activated but are immediately inhibited thereafter by selective attention. Thus, upon subsequent presentation of a previously ignored stimulus, this inhibition must be overcome, resulting in slowed processing relative to novel stimuli. The episodic retrieval model ([Neill and Valdes, 1992](#); [Neill et al., 1992](#)) proposes that ignored stimuli are fully encoded into an episodic representation, as are attended stimuli. Upon repeated presentation of a stimulus, episodic information from the initial presentation can provide a ‘shortcut’ to the previous response associated with that stimulus. Whereas this would facilitate processing of previously attended stimuli that were associated with a particular response, it is detrimental to processing of ignored stimuli with which no response was associated at study. Behavioral experiments have failed to produce unambiguous support for either of these models ([Fox, 1995](#); [May et al., 1995](#); [Egner and Hirsch, 2005](#)).

Neuroimaging can provide a useful way to test these theories, because they predict the involvement of different brain regions supporting either inhibitory or episodic processes. [Egner and Hirsch \(2005\)](#) reported data from an fMRI experiment using

a color-naming Stroop task that provide support for the episodic retrieval model. A region in the right dorsolateral prefrontal cortex (DLPFC) demonstrated increased activation for probe trials that were subject to NP relative to probe trials that had not been primed. The authors noted that this right DLPFC region has been associated with processes related to episodic retrieval (for review, see [Stevens and Grady, 2007](#)). Importantly, across individual subjects, activity in right DLPFC was positively correlated with response times during NP trials, but not nonprimed trials. These data support the theory that ignored stimuli, rather than being actively inhibited, are fully encoded at study, and that episodic retrieval at test contributes to the NP effect.

Another recent fMRI study investigated the level at which ignored stimuli are processed (i.e., perceptual vs. semantic/abstract) ([Zubicaray et al., 2006](#)). The authors reasoned that, if ignored stimuli elicit automatic activation of semantic representations at study, then brain regions that have been implicated in the storage and/or processing of these representations, such as the anterior temporal cortex (for review, see [McClelland and Rogers, 2003](#)) should be active during study of ignored stimuli. Overlapping drawings of different-colored objects elicited NP (slower reaction time for object identification at test) for previously ignored objects relative to novel objects. Analysis of fMRI data from the study session revealed a positive relationship between the magnitude of BOLD activity in the left anterolateral temporal cortex, including the temporal pole, and the magnitude of the subsequent NP effect. In agreement with [Egner and Hirsch \(2005\)](#), these data suggest that ignored stimuli are actively processed at study, and further indicate that this processing occurs at the level of abstract/semantic representations in higher conceptual brain regions.

2.33.5.2 Familiar Versus Unfamiliar Stimuli

There has been a long-standing debate in the cognitive psychology literature concerning priming of familiar versus unfamiliar stimuli (for review, see [Tenpenny, 1995](#)). According to modification/abstractionist theories ([Morton, 1969](#); [Bruce and Valentine, 1985](#)), preexisting representations are required in order for priming to occur; these abstract representations are modified in some way upon presentation of familiar stimuli. According to acquisition/episodic theories ([Jacoby, 1983](#); [Roediger and Blaxton, 1987](#); [Schacter et al., 1990](#)), priming does not rely on a preexisting

representation; rather, both familiar and unfamiliar stimuli can leave some form of a trace that can facilitate subsequent priming (although there may be limits; see [Schacter et al., 1990](#); [Schacter and Cooper, 1995](#)). Neuroimaging studies have produced data relevant to this debate.

In a PET study, [Schacter et al. \(1995\)](#) reported behavioral priming for repeated unfamiliar objects, as shown by increased accuracy of possible/impossible judgments for structurally possible three-dimensional objects. However, in contrast to the more common finding of concomitant reduction in neural activity associated with behavioral priming reviewed earlier in the chapter, the authors reported increased activation in a left inferior fusiform region that was associated with priming of the possible objects.

In a more recent event-related fMRI study, [Henson et al. \(2000\)](#) reported data from four experiments using familiar and unfamiliar faces and symbols that directly tested the hypothesis that repetition-related neural priming entails reduced neural activity for familiar stimuli, but increased neural activity for unfamiliar stimuli. Behavioral priming (faster reaction times for familiarity judgments) was documented for repetition of both familiar and unfamiliar faces and symbols (although priming was greater for familiar than for unfamiliar stimuli). However, in a right fusiform region, repetition resulted in decreased activation for familiar faces and symbols, but increased activation for unfamiliar faces and symbols.

[Henson et al. \(2000\)](#) offered an account of their findings in terms of both modification and acquisition: while priming of familiar stimuli involves modification of preexisting representations, resulting in repetition suppression, priming also occurs for unfamiliar stimuli as a new representation is formed, resulting in repetition enhancement (for a generalized theory, see [Henson, 2003](#)). This suggestion is supported by evidence from a study by [Fiebach et al. \(2005\)](#), who concluded that neural decreases accompanying repeated words, in contrast to neural increases accompanying repeated pseudowords, reflect the sharpening of familiar object representations and the formation of novel representations for unfamiliar objects, respectively. Further, data from a previously reviewed study by [Ishai et al. \(2004\)](#) support this hypothesis as well; for unfamiliar faces, neural activation increased for the first repetition, but decreased in a linear trend thereafter, possibly reflecting the initial acquisition of an unfamiliar face representation, followed by subsequent modification of this newly

formed representation. Henson et al. (2000) further hypothesized that the repetition enhancement effect for unfamiliar stimuli would only occur in “higher visual areas, such as the fusiform cortex, where the additional processes such as recognition occur” (Henson et al., 2000: 1272). However, in a recent study using event-related fMRI, Slotnick and Schacter (2004) reported increased activation in early visual processing regions (BA 17/18) for repeated, relative to novel, unfamiliar abstract shapes. This finding suggests that earlier perceptual regions may also demonstrate activation attributable to processes involved in acquisition of new representations of unfamiliar stimuli.

2.33.5.3 Sensitivity Versus Bias

In number of studies by Schacter and colleagues (Schacter et al., 1990, 1991a; Cooper et al., 1992; Schacter and Cooper, 1993) participants studied line drawings of structurally possible and impossible objects and then made possible/impossible judgments at test to repeated presentations of the objects. Behavioral priming is measured as increased accuracy (and/or faster reaction time) for identifying an object as possible or impossible upon repeated presentations; significant priming is consistently observed for possible, but not impossible, objects. As mentioned earlier, a PET study of priming on the possible/impossible decision task revealed that increased activation in a left inferior/fusiform region was associated with priming of possible objects only (Schacter et al., 1995).

Schacter and Cooper proposed that such priming depends on the structural description system (SDS), a subsystem of the more general perceptual representation system (Tulving and Schacter, 1990). The proposal of an SDS was based on evidence of dissociations between priming (for possible, but not impossible, objects) and explicit tests of memory, across study-to-test object transformations (Cooper, et al., 1992; Schacter et al., 1993b), manipulations at encoding (Schacter and Cooper, 1993; Schacter et al., 1990), and in studies with elderly populations and amnesic patients (Schacter et al., 1991b, 1992, 1993b; and for review, see Soldan et al., 2006). In this view, priming of repeated objects reflects increased sensitivity (i.e., accuracy) on the part of the SDS, which is only capable of representing structurally possible objects.

An alternative theory is the bias account of priming in the possible/impossible object-decision task proposed by Ratcliff and McKoon (McKoon and

Ratcliff, 1995, 2001; Ratcliff and McKoon, 1995, 1996, 1997, 2000). In this view, an encounter with an object, regardless of whether it is structurally possible or impossible, results in a subsequent bias to classify that object as ‘possible,’ leading to increased accuracy (i.e., positive priming) for repeated possible objects but decreased accuracy (i.e., negative priming) for impossible objects. However, this account also posits that explicit processes play a role in object-decisions, such that explicit memory of the study episode cues subjects as to whether the object is possible or impossible. It is argued, then, that this combination of bias and episodic information leads to robust positive priming for possible objects. By contrast, for impossible objects, the two factors cancel each other out, resulting in zero priming. Ratcliff and McKoon (1995) reported data from seven experiments that supported their hypothesis (for criticism of their conclusions, see Schacter and Cooper, 1995; for response, see McKoon and Ratcliff, 1995). Other bias accounts of object-decision priming have been proposed as well, such as the structure-extraction bias (Williams and Tarr, 1997).

Behavioral studies relevant to this debate continue to emerge, supporting either the sensitivity account of priming (e.g., Zeelenberg et al., 2002) or the bias account (e.g., Thapar and Rouder, 2001), but behavioral investigations alone have been inconclusive (Soldan et al., 2006). However, neuroimaging studies have recently produced evidence that speaks to the ongoing debate.

In a recent event-related fMRI study (Habeck et al., 2006), subjects performed a continuous possible/impossible object-decision task on structurally possible and impossible objects repeated four times each. Although the behavioral results did not correspond to sensitivity or bias models, or to previous findings (priming, as measured by faster reaction times, was documented for both possible and impossible objects), neural priming was documented for possible objects only. A multivariate analysis of the fMRI data revealed a pattern of brain regions in which activation covaried in a linear fashion (areas showing both repetition suppression and repetition enhancement) with repetition of possible objects only. No such pattern was observed for repetition of impossible objects. Further, there was a correlation between behavioral (faster reaction times) and neural priming for possible objects only.

Similarly, a recent ERP study by Soldan et al. (2006) reported data from two possible/impossible object-decision priming experiments using unfamiliar

objects that provide compelling evidence that the visual system differentially encodes globally possible versus globally impossible structures. In the first experiment, subjects made structural decisions (right/left orientation-decision task) about possible and impossible objects at study. In the second experiment, a functional decision (tool/support function-decision task) was performed at study. The behavioral results of the experiments were inconclusive with respect to sensitivity versus bias theories. However, the ERP data clearly failed to support bias theories, which hold that possible and impossible objects are processed similarly in the visual processing system. Rather, two early ERP components (the N1 and N2 responses) showed repetition enhancement for possible objects, but no neural effect for repetition of impossible objects, in both the structural and functional encoding experiments. Moreover, the magnitude of repetition enhancement in the N1 ERP component was correlated with behavioral priming for possible objects. These data support the theory that priming is supported by an SDS that encodes structurally possible objects only.

2.33.6 Correlations between Behavioral and Neural Priming

While neuroimaging studies have provided considerable evidence bearing on the neural correlates of priming, caution is warranted when interpreting the causal nature of such effects. Although a number of studies have documented the close overlap between neuronal activity and BOLD activity in the primate (Logothetis et al., 2001; Shmuel et al., 2006; for a human analogue see Mukamel et al., 2005), it is critical to determine whether functional neuroimaging data reflect the neural underpinnings of cognitive processes or index spurious activations that are epiphenomenal to the process of interest.

Initial studies used methodologies where blocks during which participants viewed repeated items were contrasted with blocks during which participants viewed novel items (e.g., Squire et al., 1992; Raichle et al., 1994; Buckner et al., 1995; Schacter et al., 1996; Wagner et al., 1997). The introduction of event-related fMRI (Dale and Buckner, 1997) later allowed researchers to intermix old and new items and delineate activity associated with individual trial-types, providing evidence that the neural priming that accompanies repeated items is not simply due to a blunting of attention or vigilance that may

permeate extended periods of cognitive processing (e.g., Buckner et al., 1998). Together, studies of this sort have consistently documented the co-occurrence of behavioral priming and neural priming in a subset of the brain regions that are engaged during task performance with novel material (see Figure 1).

In order to establish a link between neural priming and behavioral priming, neuroimaging studies have attempted to demonstrate a relationship between the magnitude of both effects. That is, if neural priming is indeed related to behavioral priming, then the two should not only co-occur but should be directly correlated. A number of studies have reported a positive correlation between the magnitudes of behavioral priming and neural priming in frontal regions during tasks of a semantic or conceptual nature. Maccotta and Buckner (2004) showed that behavioral priming for repeated words in a living/nonliving classification task was significantly correlated with the magnitude of neural priming in regions of the left inferior frontal gyrus and pre-supplementary motor areas. Using the same task, Lustig and Buckner (2004) documented significant correlations between behavioral and neural priming in the left inferior frontal gyrus for young adults, healthy older adults, and patients with Alzheimer's disease (also see Golby et al., 2005). A similar pattern has been documented in the auditory domain: Orfanidou et al. (2006) found that the degree of auditory word priming on a lexical decision task was predicted by the extent of neural priming in left inferior frontal gyrus and supplementary motor areas. Others have found that the correlation between behavioral priming and prefrontal neural priming can be category specific. Using a classification task, Bunzeck et al. (2006) provided evidence that the correlations between neural and behavioral priming were specific for scenes in left inferior prefrontal cortex, but for faces in left middle frontal gyrus.

Consistent with the foregoing findings, in the aforementioned study by Dobbins et al. (2004), multiple regression analysis revealed that left prefrontal activity predicted the disruptive effects of response switching on behavioral priming for individual subjects: greater initial reductions in prefrontal activity were associated with greater subsequent disruptions of behavioral response times when the response was changed. To the extent that activation reductions in prefrontal cortex indicate less reliance on controlled processing and greater reliance on automatic processing, these data suggest that performance disruptions attributable to response switching reflect a need to

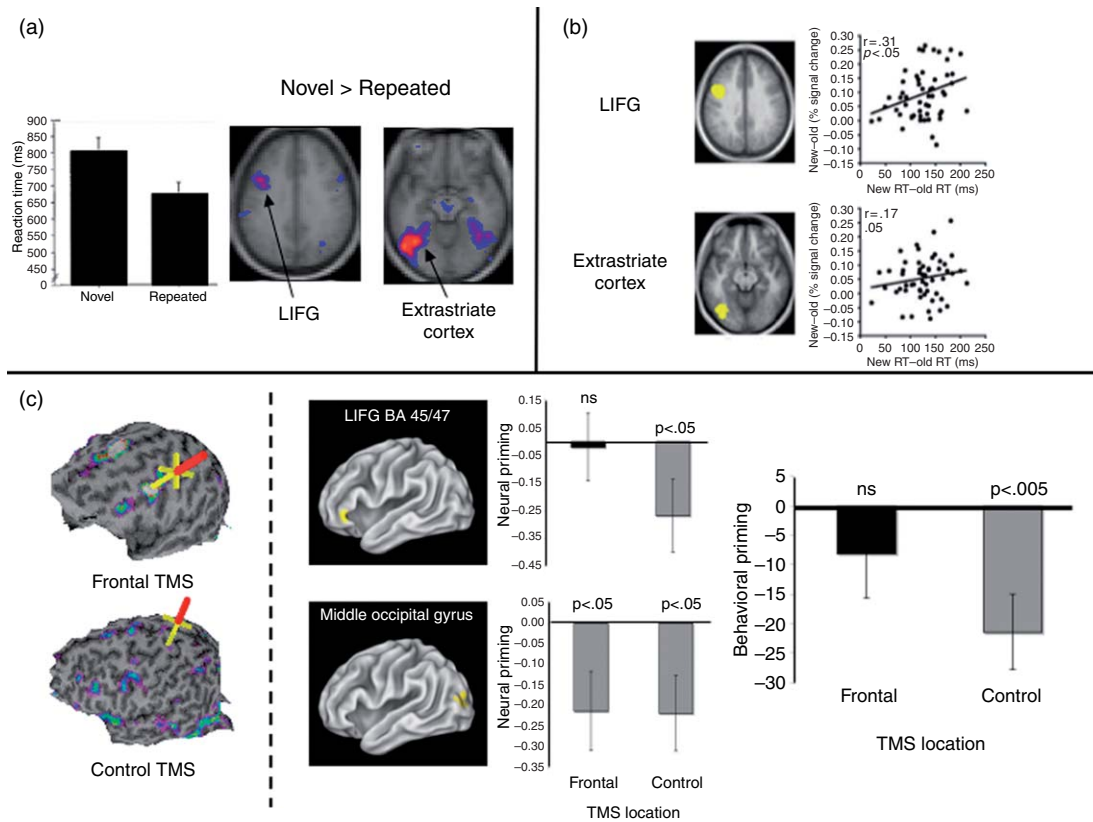


Figure 1 Correlations between behavioral and neural priming. (a) Semantic classification of visual objects using event-related fMRI reveals that the decrease in response time (behavioral priming) that accompanies classification of repeated items co-occurs with decreased activity (neural priming) in regions of the left inferior frontal gyrus (LIFG) and extrastriate cortex. (b) During semantic classification of words, the magnitude of behavioral priming is directly correlated with the magnitude of neural priming in the LIFG, but not the extrastriate cortex. (c) Transcranial magnetic stimulation (TMS) applied to a region of the LIFG (but not of a control location) during semantic classification of visual objects disrupts subsequent behavioral priming and the neural priming in LIFG during fMRI scanning. Neural priming in the middle occipital gyrus is unaffected by frontal or control TMS. Adapted from (a) Buckner RL, Goodman J, Burock M, et al. (1998) Functional-anatomic correlates of object priming in humans revealed by rapid presentation event-related fMRI. *Neuron* 20: 285–296, with permission from Elsevier; (b) Maccotta L and Buckner RL (2004) Evidence for neural effects of repetition that directly correlate with behavioral priming. *J. Cogn. Neurosci.* 16: 1625–1632, with permission from MIT Press; (c) Wig GS, Grafton ST, Demos KE, and Kelley WM (2005) Reductions in neural activity underlie behavioral components of repetition priming. *Nat. Neurosci.* 8: 1228–1233, with permission from the authors.

reengage slower controlled processes in order to make object decisions. This idea is consistent with the further finding that reductions in fusiform activity did not predict behavioral costs of switching cues, suggesting that these reductions may be incidental to behavioral priming during conceptual tasks.

Other evidence indicates that behavioral priming can correlate with neural priming in regions outside the prefrontal cortex as well. Bergerbest et al. (2004) found that behavioral priming for environmental sound stimuli correlated with neural priming in right inferior prefrontal cortex and also in two secondary auditory regions: bilateral superior temporal

sulci and right superior temporal gyrus. Using a stem completion task, Carlesimo et al. (2003) found that the magnitude of behavioral cross-modality priming (auditory-to-visual) was correlated with the extent of activation reduction at the junction of the left fusiform and inferior temporal gyrus.

Turk-Browne et al.'s (2006) study of the relation between priming and subsequent memory effects, (where, as discussed earlier, neural activity during encoding is sorted according to whether items are subsequently remembered or forgotten) provided a different perspective on the correlation issue. Repeated scenes produced behavioral and neural

priming, but only for those scenes that were subsequently remembered. For these scenes only, there was also a correlation between the magnitude of behavioral and neural priming in the fusiform gyrus; this relationship approached significance in right inferior prefrontal cortex. As discussed earlier, the finding that the degree of behavioral and neural priming depended on subsequent memory points toward a link between implicit and explicit memory, perhaps involving shared attentional processes.

Together, these studies provide evidence for a relationship between behavioral priming and neural priming (also see Zago et al., 2005; Habeck et al., 2006). Correlations between the two variables generalize across paradigms (e.g., semantic classification, stem-completion) and are restricted to regions thought to mediate the cognitive operations engaged during the task. Although these correlations have been consistently reported with respect to neural priming in frontal cortices and to a lesser extent temporal cortex, few studies thus far have provided evidence for a correlation between behavioral priming and neural priming in earlier perceptual cortices – even though neural priming in the latter regions frequently accompanies item repetition.

The relationship between behavioral priming and neural priming in early visual regions was explicitly explored by Sayres and Grill-Spector (2006). Participants were scanned using fMRI in an adaptation paradigm during a semantic classification task on objects. Repetition of objects was accompanied by reductions in activity in regions of the LOC and posterior fusiform gyrus. However, in contrast to the correlations that have been observed between neural and behavioral priming in frontal and temporal regions, neural priming in earlier visual regions was unrelated to the facilitation in response time that accompanied repeated classification, thus providing more evidence that these two phenomena may be less tightly associated in these regions.

Although these correlations suggest that neural priming effects in prefrontal and temporal regions may support behavioral priming on a number of tasks, they do not allow conclusions regarding a causal role. It is possible that neural priming in these regions is necessary for behavioral priming. Alternatively, neural priming in other areas of the brain (e.g., regions of perceptual cortex) may subservise behavioral priming, and the neural priming observed in prefrontal and temporal cortex may simply reflect a feedforward propagation of the changes occurring in these other regions. In order to establish

a causal relationship between behavioral priming and neural priming in frontal and temporal cortex, one would have to provide evidence of a disruption of behavioral and neural priming in these regions, accompanied by intact neural priming in perceptual cortices.

Wig et al. (2005) provided such evidence by combining fMRI with transcranial magnetic stimulation (TMS). TMS allows for noninvasive disruption of underlying cortical activity to a circumscribed region, thus inducing a reversible temporary virtual lesion (Pascual-Leone et al., 2000). In the study by Wig and colleagues, for each participant, regions of the left prefrontal cortex (along the inferior frontal gyrus) that demonstrated neural priming were first identified during semantic classification (living/nonliving) of repeated objects using fMRI. Each participant was then brought back for a TMS session where they classified a new set of objects using the same task. Short trains of TMS were applied to the previously identified prefrontal region during classification of half of these objects; classification of the remaining half of objects was accompanied by TMS applied to a control region (left motor cortex). Immediately following the TMS session, subjects were rescanned with fMRI while performing the semantic classification task on objects that were previously accompanied by prefrontal stimulation, objects previously accompanied by control-site stimulation, and novel objects. Results revealed that classification of objects that had been previously accompanied by left frontal TMS failed to demonstrate subsequent behavioral priming and neural priming in the left inferior frontal gyrus and lateral temporal cortex. By contrast, neural priming in early visual regions remained intact. Critically, these effects were not due to generalized cortical disruption that accompanied TMS; control-site stimulation had no disruptive effects on either behavioral or neural markers of priming. Consistent with this finding, Thiel et al. (2005) provided evidence for a disruptive effect of left-frontal TMS on behavioral priming during a lexical decision task. Together, these results provide evidence that behavioral and neural markers of priming in frontal and temporal regions are causally related, not just correlated.

In summary, correlations between behavioral and neural priming are observed consistently in prefrontal, and to some extent temporal, regions on priming tasks that include a conceptual component, such as semantic classification and stem completion. Although studies using such tasks have failed to

demonstrate a relationship between behavioral priming and neural priming in perceptual regions, behavioral demonstrations of perceptual priming are well documented (e.g., [Tulving and Schacter, 1990](#); [Schacter et al., 1993a](#)). A key hypothesis to be evaluated in future investigations is that neural priming in perceptual cortices subserves perceptual priming. Establishing a causal relationship between the two necessitates careful consideration of the behavioral tasks used to demonstrate such effects. Further, it is likely that the behavioral advantage for repeated processing of an item is mediated by multiple processes and components of priming – both conceptual and perceptual – that contribute in an aggregate fashion to facilitate task performance (e.g., [Roediger et al., 1999](#)). Neuroimaging research can be helpful in attempting to tease apart the components of such effects and link them with the activity of specific brain regions.

2.33.7 Summary and Conclusions

Our review demonstrates that neuroimaging research has shed new light on cognitive theories of priming that were originally formulated and investigated through behavioral approaches within the field of cognitive psychology. The contributions of this research include advances with respect to long-standing theoretical debates about the nature of priming, as well as new lines of investigation not previously addressed by cognitive studies.

As alluded to earlier, evidence across several domains of neuroimaging research on priming is inconsistent with a single process account of the phenomenon, and instead supports the idea that multiple processes are involved in different types of behavioral priming and corresponding neural priming. [Schacter et al. \(2007\)](#) recently proposed a multiple-component view of priming, as depicted in [Figure 2](#).

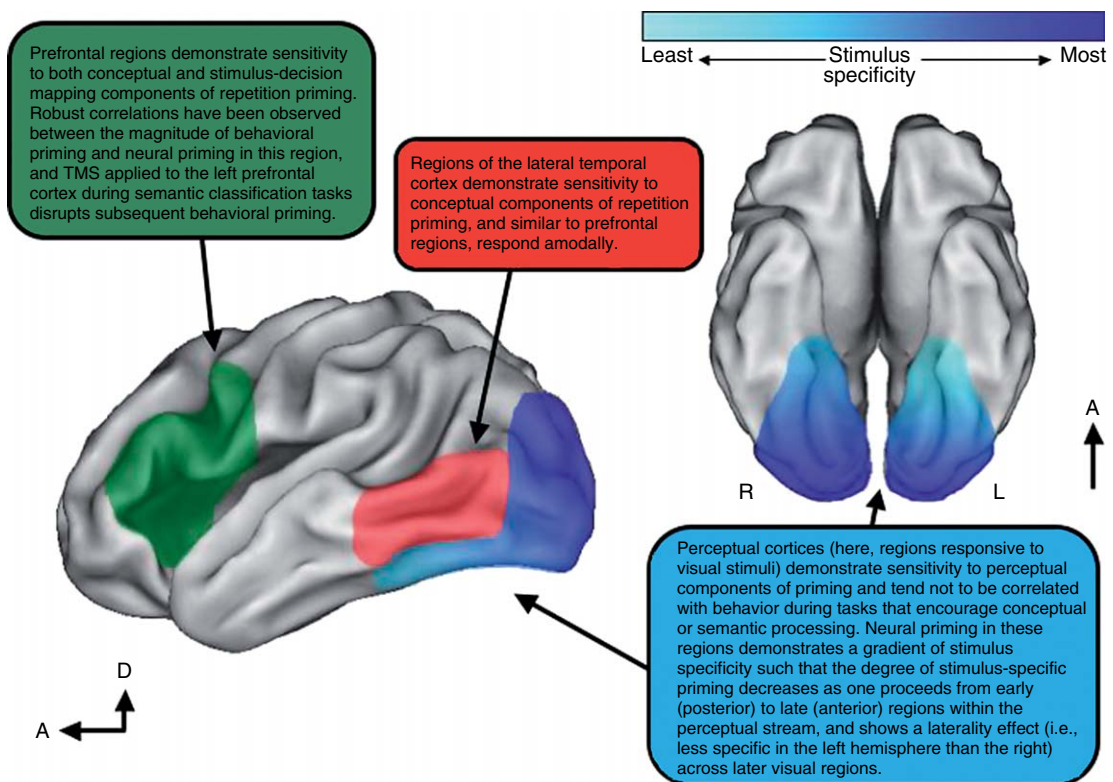


Figure 2 Schematic of proposed components of priming. Figure depicts partially inflated lateral view of the left hemisphere and ventral view of the left and right hemispheres. Lateral view is tilted in the dorsal-ventral plane to expose the ventral surface ('A' denotes anterior direction, 'D' denotes dorsal direction, 'L' and 'R' denote left and right hemispheres, respectively). Color-coding of anatomical regions is meant to serve as a heuristic for the proposed components. The color gradient within the ventral visual stream (blue) is meant to represent approximately the gradient of stimulus specificity that has been observed within these regions. TMS, transcranial magnetic stimulation. Adapted from [Schacter DL, Wig GS, and Stevens WD \(2007\) Reductions in cortical activity during priming. *Curr. Opin. Neurobiol.* 17: 171–176](#), with permission from Elsevier.

This view suggests that there are at least two distinct mechanisms involved in neural priming. One corresponds roughly to what Wiggs and Martin (1998) called *sharpening* or *tuning*, which occurs when exposure to a stimulus results in a sharper, more precise neural representation of that stimulus (See Chapter 3.12; see also Grill-Spector et al. (2006) for more detailed consideration of sharpening and related ideas). Such tuning effects are likely to predominate in posterior regions that code for the perceptual representations of items, and perhaps in anterior regions that underlie conceptual properties of these items. Tuning effects, however, are unable to account for response-specific priming effects (e.g., Dobbins et al., 2004) and appear to be less correlated with behavioral priming observed during tasks that are semantic or conceptual in nature. The second proposed mechanism primarily reflects changes in prefrontal cortex that drive behavioral priming effects in a top-down manner, as initially controlled processes become more automatic (Logan, 1990; Dobbins et al., 2004).

While the view proposed by Schacter et al. (2007) suggests two possible components of priming, this is a preliminary model that needs to be extended, elaborated, and related more fully to distinctions among types of priming (e.g., perceptual, conceptual, associative) that have been long discussed in the cognitive literature. Traditional theories of priming laid the groundwork for understanding these components, and neuroimaging research will likely play a crucial role in resolving the questions that remain, in suggesting new lines of inquiry not previously conceived of, and in expanding our understanding of the nature of priming and implicit memory more generally.

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