

# Neuroanatomical Organization of Perceptual Memory: An fMRI Study of Picture Priming

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**Abstract:** Neuroanatomical organization of perceptual representation in human memory system is unclear primarily because it has been studied using paradigms that have both, perceptual and conceptual components (e.g., word stem completion and word fragment completion). In the present experiment, functional magnetic resonance imaging (fMRI) technique was used to examine the pattern of cortical activation in a picture identification test in which subjects were asked to identify subliminally presented primed and novel pictures. This test is a modification of the word identification test that is considered a “pure” form of perceptual priming. Results indicate that perceptual priming is associated with reduced activation in the extrastriate cortex and that the memory for subliminally presented stimuli is processed by the same brain areas that process adequate stimuli. The activation pattern observed in picture identification test is different from that reported in the experiments of conceptual priming, suggesting that perceptual and conceptual representation of memory are supported by separate brain mechanisms. *Hum. Brain Mapping* 10:197–203, 2000. © 2000 Wiley-Liss, Inc.

**Key words:** implicit memory; subliminal stimuli; perceptual representation; extrastriate cortex; area V3A; temporal cortex; picture identification test

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Neuroimaging and neuropsychological studies distinguish two forms of memory: explicit and implicit. Whereas explicit memory is a conscious process by which past experiences are recalled, implicit memory is considered a nonconscious process and is described as a change in the ability to identify or produce an item as a consequence of a specific prior encounter

[Tulving and Schacter, 1990]. Implicit memory has been studied using a variety of laboratory tests [for review, see Schacter et al., 1993]. These tests include a number of priming paradigms. In a typical priming experiment, subjects first study a list of target items and later perform a task that requires them to identify, produce, or make a decision about studied and non-studied items. It has been demonstrated that in priming experiments, cues that are perceptually or conceptually similar to the studied items have distinct retrieval advantages. Thus, a significantly higher percentage of studied item is retrieved when test items either have similar perceptual features (e.g., same font/case, or same voice) [Bassili et al., 1989; Schacter and Church, 1992], or are conceptually associated with

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Contract grant sponsor: NIH; Contract grant numbers: R01 MH60941 and MH57915; Contract grant sponsor: MacArthur Foundation.

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Received for publication 30 September 1999; accepted 9 May 2000

the studied items (e.g., doctor-hospital) [Meyer and Schvaneveldt, 1971]. Because the tasks that are dependent on perceptual or conceptual representation are processed differently, there are two forms of priming—perceptual and conceptual [Schacter and Buckner, 1998; Schacter et al., 1993].

Current understanding of the cortical correlates of perceptual priming is based mainly on the experiments that have used a word stem completion task [Backman et al., 1997; Badgaiyan and Posner, 1996, 1997; Badgaiyan et al., 1999; Buckner et al., 1995; Schacter et al., 1996; Squire et al., 1992]. In this task, subjects first study a list of words, and later they are asked to complete word stems using the first word that comes to mind. A word stem is either the first three-letter (visual word stem) or the first syllable (auditory word stem) of a studied target word. Due to the priming effect, subjects typically complete stems using a studied word, even though each stem has multiple possible completions.

In a word stem completion task, priming effects are observed both, when target words are studied and tested in the same (within-modality priming) or in a different sensory modality (cross-modality priming). It is believed that the cross-modality priming is not dependent on perceptual representation because there are no perceptual similarities between the study and test stimuli. It probably depends on conceptual representation [Bassili et al., 1989]. In within-modality priming, the study and test items could have the same or different perceptual features. For example, in visual word stem completion tasks, if the same fonts and letter-cases are used in the study and test, perceptual features would be the same, but by using a different font or case in the test, the features could be changed between study and test. In these experiments, even though a priming advantage has been observed when study and test items share similar perceptual features [Bassili et al., 1989; Schacter and Church, 1992], the performance is not dependent solely on perceptual representation. It is influenced significantly by semantic and lexical processing [Richardson-Klavehn and Gardiner, 1998; Schacter and Buckner, 1998; Wiggs and Martin, 1998]. These influences indicate that a within-modality stem completion task has a conceptual component in addition to a perceptual component [Schacter and Buckner, 1998; Wiggs and Martin, 1998].

Another perceptual priming task that has been used in neuroimaging studies is a word fragment completion task [Blaxton et al., 1996]. In this task, subjects first study a list of words, and later they are asked to complete a fragmented target word by filling in blank

spaces (e.g., P\_CT\_R\_). Like the stem completion, this task is also influenced by semantic and lexical processing, and involves both perceptual and conceptual representation [Schacter et al., 1993]. Thus, neuroimaging studies that have used a within-modality stem completion or a word fragment completion task do not provide conclusive neuroanatomical information on either perceptual or conceptual representation. Therefore, even though these studies have consistently reported reduced activity in the extrastriate area [Backman et al., 1997; Badgaiyan and Posner, 1996, 1997; Badgaiyan et al., 1999; Blaxton et al., 1996; Buckner et al., 1995; Schacter et al., 1996; Squire et al., 1992], the question whether this reduction is associated with perceptual or conceptual priming remains unclear.

Present experiment was conducted to examine whether reduced extrastriate activity is associated with perceptual priming. A functional magnetic resonance imaging (fMRI) technique was used to study the pattern of cortical activation in a picture identification test which is similar to a word identification test—considered to be a “pure” form of perceptual priming [Jacoby and Hayman, 1987; Schacter and Buckner, 1998]. In a word identification test, subjects first study a list of target words. Later, target and novel words are presented subliminally and subjects are asked to identify words. Subliminal presentation typically allows better identification of a studied word. In the present study, words were replaced by pictures to reduce the effect of lexical processing that may be associated with a word identification test. The pattern of cortical activity observed during subliminal presentation of primed pictures was compared with that observed during subliminal presentation of unprimed (baseline) pictures. The activations were also compared with those obtained during a look-only condition in which subjects looked at the novel pictures presented for 3 sec. The look-only condition was introduced to identify the baseline pattern of cortical activity associated with visual processing of pictures. Subtraction of this baseline from the patterns obtained during the presentation of primed and unprimed pictures would help identify the cortical areas associated with execution of tasks that are common in the two conditions. These tasks could include identification and semantic processing of presented pictures. In this experiment, because a test of “pure” perceptual priming was used, finding of a reduced extrastriate activation would associate the reduction with perceptual priming.

## MATERIALS AND METHODS

The study was conducted on ten healthy, young volunteers (mean age 19.9 years; six females) using an fMRI technique. The protocol was approved by the institutional review board and informed consents were obtained from all volunteers. They were right-handed when tested using a modified Edinburgh handedness criteria [Raczkowski et al., 1974]. The exclusion criteria included a history of psychiatric or neurological disorder, prolonged use of a recreational or prescription drug, claustrophobia, and a metal or pacemaker implant. Subjects were advised to remain alcohol-free at least 24 hr prior, and tobacco-free at least 3 hr prior to the scan time.

At the study stage, a series of achromatic line drawings of common objects, animals, and plants was presented (3 sec each) and subjects were asked to indicate by pressing a key whether they liked the picture. In each study block, 120 pictures were presented in such a way that the first and the last ten pictures were always nontarget "filler" pictures which were included to reduced primacy and recency effects. There were 100 target pictures in each block. Two minutes following the study, tests began. At this stage, subjects were shown target and novel pictures subliminally (16 msec each; ISI 2984 msec) and were asked to indicate, by pressing a response key (using the right hand) whether they could identify the object in a picture. In a pilot study conducted out of scanner, subjects were able to identify 81.8% of primed and 5.1% of unprimed pictures following subliminal presentation.

Functional images were obtained at the test stage under three conditions: priming (studied pictures), baseline (novel pictures), and look-only. In the look-only condition, novel pictures were presented for 3 sec and subjects were instructed to look at the pictures but not to make any response. There were two study blocks, each of which was followed by two test blocks. Each test block had 124 pictures (50 primed, 50 baseline, and 24 look-only). Each subject had four scan blocks. A 2-min rest period was allowed between test blocks and between a test and a study block. The presentation sequence of test conditions was counterbalanced across scan blocks and subjects. Pictures were also counterbalanced across subjects to ensure that each picture is presented equally often in all test conditions. Response time was recorded both at the study and test stage, using a PsyScope button box [Macwhinney et al., 1997].

After subjects were comfortably placed in the scanner, earplugs were provided to reduce the effect of background scanner noise. Thereafter, images were

obtained using a 1.5 tesla GE signa scanner. For anatomical localization of activity, T1 weighted structural images were acquired (spin echo pulse sequence, TR 500 msec, TE 16 msec, FOV 20 cm) in coronal plane. Functional (T2\* weighted) images were also obtained in coronal plane at 28 slice locations (echo planar gradient echo sequence, 5 mm thick, 0 skip; TR = 6,000 msec, TE = 40, flip angle = 90°, FOV = 20 cm, 3.125 × 3.125 × 5 mm in-plane resolution, 64 × 64 matrix). Images were motion corrected using an automated image registration algorithm [Woods et al., 1992] and magnetic resonance signal intensity obtained during each condition was compared using pixel-wise analysis of variance (contiguity threshold, 5 pixels;  $p < .001$ ). Images were transformed into Talairach space [Talairach and Tournoux, 1988] and merged across subjects.

## RESULTS AND DISCUSSION

Behavioral data confirmed the priming effect. Primed pictures elicited greater recognition ( $p < 0.0001$ ) and faster response ( $p < 0.05$ ) as compared to novel pictures. Specifically, subjects identified  $95.4 \pm 2.4\%$  of primed and  $5.6 \pm 2.4\%$  of novel pictures. Mean reaction times for primed and novel pictures were  $754 \pm 27$  and  $828 \pm 46$  msec, respectively. The percentage of primed pictures identified in the present experiment was higher than the percentage of words that are typically identified in a word identification task [Jacoby and Hayman, 1987; Rajaram and Roediger, 1993]. It could be due to the picture superiority effect that predicts greater recollection of studied pictures than studied words under similar retrieval conditions [Madigan, 1983; Mintzer and Snodgrass, 1999; Paivio and Csapo, 1973]. However, the magnitude of priming effects observed in the present experiment suggests that greater recognition could be due to the blocked design of this experiment. Even though each block had both primed and unprimed pictures, the presentation sequence was not intermixed. All of the primed and unprimed pictures were presented sequentially in each block.

In the look-only condition, subjects did not make any response. They were asked just to look at the pictures presented every 3 sec. In the priming and baseline conditions, they had to look at the picture and, at the same time, make a response indicating whether they had identified it. Because responses were made using the right hand, the intensity of magnetic resonance was greater in the left primary motor cortex (Brodmann's area; BA 4) both in the priming and baseline condition in comparison with the look-

**TABLE I. Regions showing significant rCBF changes in a picture recognition task**

Condition and cortical area		Talairach coordinates <i>x,y,z</i>
Priming minus look-only		
rCBF decrease	Extrastriate cortex (BA 19)	27,-84,28
rCBF increase	Primary motor cortex (BA 4)	-45,-11,29
	Prefrontal cortex (BA 45/46)	39,35,7
	Prefrontal cortex (BA 45/46)	-36,37,11
Baseline minus look-only		
rCBF increase	Primary motor cortex (BA 4)	-52,-9,35
	Prefrontal cortex (BA 45/46)	46,32,9
	Prefrontal cortex (BA 45/46)	-44,37,22
rCBF decrease	None	
Priming minus baseline		
rCBF decrease	Extrastriate cortex (BA 19)	21,-82,20
rCBF increase	None	

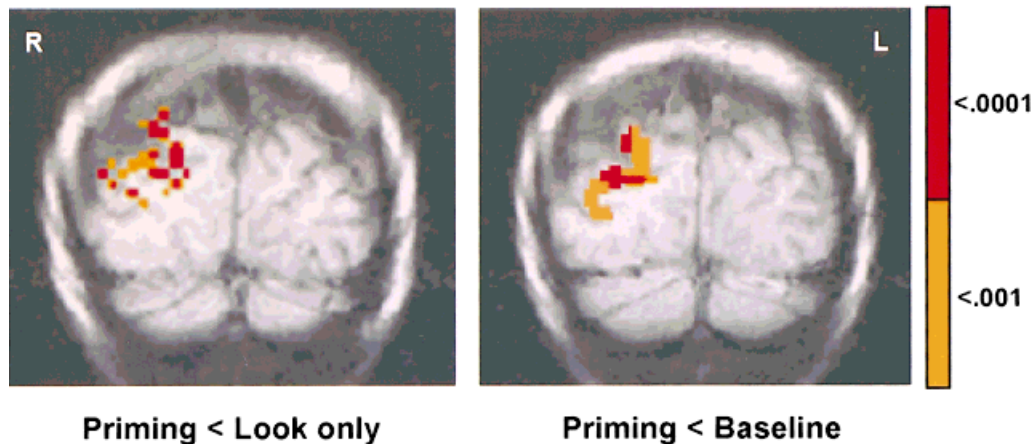
only condition. In addition, there was increased magnetic resonance intensity in the dorsolateral prefrontal cortex (BA 46/45) in both (priming and baseline) conditions (Table I). There was no area of reduced intensity in the baseline condition as compared to the look-only condition. In the priming condition, however, there was significantly reduced magnetic resonance intensity in the right extrastriate cortex (BA 19) when

compared either with the baseline or look-only condition (Fig. 1).

This observation is significant because reduced extrastriate activity is the only common pattern reported in the tests that involve perceptual representation. These tests include stem completion [Backman et al., 1997; Badgaiyan and Posner, 1996, 1997; Badgaiyan et al., 1999; Buckner et al., 1995; Schacter et al., 1996, 1999; Squire et al., 1992] and word fragment completion [Blaxton et al., 1996] tasks. We have recently observed reduced activation in BA 19 in an auditory priming experiment in which subjects studied a list of words aurally and were asked to complete auditory word stems [Badgaiyan et al., 1999]. This observation suggests that even though the extrastriate is a part of the visual system and a large proportion of neurons in this area is involved in visual information processing, it is unlikely that the reduction observed during priming is associated with visual information processing because no visual stimulus was used in this experiment.

We have recently characterized the nature of the extrastriate involvement in perceptual priming by conducting another auditory priming experiment in which word stems were presented either in the same voice in which target words were studied or in a different voice [Badgaiyan et al., 2000]. We found reduced regional cerebral blood flow (rCBF) in the extrastriate area in both, same voice and different voice,

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**Figure 1.**

In a picture identification test, a reduction in the intensity of magnetic resonance was observed in the extrastriate area (BA 19) following subliminal presentation of primed pictures. The reduction was significant both in comparison with the baseline (novel picture) and look-only condition. The stereotaxic coordinates were: 27, -84, 28 (priming < look-only) and 21, -82, 20 (priming < baseline).

conditions. Similar findings have been reported in visual domain. Thus, reduced activity in the extrastriate area was observed when the letter-case (upper or lower) was changed between study and test [Badgaiyan and Posner, 1996, 1997; Buckner et al., 1995]. These findings indicate that the extrastriate system recognizes a within modality cue even when it is presented in a different form.

The observation of an increased prefrontal activation in both priming and baseline conditions in the present experiment is intriguing particularly because these activations are typically associated with explicit retrieval [Badgaiyan and Posner, 1997; Gabrieli, 1998; Schacter et al., 1997; Tulving et al., 1996]. Because the activation was observed in both priming and baseline conditions, clearly it is not associated with priming but reflects additional processing that are necessary in both priming and baseline conditions but not in the look-only condition. Because pictures were presented subliminally in priming and baseline conditions and for 3 sec in the look-only condition, prefrontal activation is possibly associated with the cortical processing that is necessary to identify subliminally presented pictures. Interestingly, we have earlier observed similar prefrontal activation in the different voice condition described previously. It was speculated that this activation is a part of a "second cycle" of search that is activated when a mismatch is indicated between perceptual properties of a test cue and those of a previously studied item [Badgaiyan et al., 2000]. A study to test mismatch probably necessitates "normalization" of the test stimuli (by the "second cycle") to allow their recognition by the extrastriate system. This process of normalization is activated only if a mismatch is detected within the same sensory modality. When the mismatch involves changes across modalities (as in cross-modality priming), the extrastriate system is not involved [Badgaiyan et al., 1999; Schacter et al., 1999].

In the present study, there is no perceptual mismatch between study and test stimuli. There is, however, a temporal mismatch. Stimuli are presented for 3 sec in the study and for 16 msec in priming and baseline conditions. The observation of increased prefrontal activation in both priming and baseline conditions is an interesting finding that requires further investigation to examine whether a study-to-test change in the "temporal feature" activates the same cortical areas that detect similar changes in surface features (e.g., font/case or voice) of stimuli. The observation of reduced extrastriate activation in the present experiment underscores another significant point—subliminally presented stimuli are processed by the same brain areas that process adequate stimuli.

Another study in which we examined the role of extrastriate and prefrontal areas in priming involved cross-modality priming conditions [Badgaiyan et al., 1999; Schacter et al., 1999]. In these experiments, we scanned subjects while they provided completions to auditory or visual word stems after studying target words either in the same (within-modality) or in a different sensory modality (cross-modality). Reduction in the extrastriate rCBF was observed in within-modality (visual-to-visual, and auditory-to-auditory) but not in cross-modality conditions (visual-to-auditory, and auditory-to-visual), even though the two conditions elicited similar degrees of priming. Because cross-modality priming is not dependent on perceptual representation [Bassili et al., 1989], reduced activation of the extrastriate cortex seems to be associated specifically with retrieval of perceptually driven information. This association is particularly remarkable because the reduction has been reported in a variety of tests involving perceptual representation. These tests include word stem completion [Backman et al., 1997; Badgaiyan and Posner, 1996, 1997; Badgaiyan et al., 1999; Buckner et al., 1995; Schacter et al., 1996; Squire et al., 1992], word fragment completion [Blaxton et al., 1996], object repetition [Buckner et al., 1998], and picture identification (present study) tasks. Further, these tests were conducted using two different sensory modalities—visual [Backman et al., 1997; Buckner et al., 1995; Schacter et al., 1996, 1999; Squire et al., 1992], and auditory [Badgaiyan et al., 1999, 2000], and three different neuroimaging techniques—event-related potentials [Badgaiyan and Posner, 1996, 1997], positron emission tomography [Backman et al., 1997; Badgaiyan et al., 1999, 2000; Blaxton et al., 1996; Buckner et al., 1995; Schacter et al., 1996, 1999; Squire et al., 1992], and fMRI [Buckner et al., 1998; and the present study].

Neuroanatomical and neurophysiological evidence suggest that at least a part of the extrastriate cortex has a multimodal function. This evidence is significant because it may be necessary for a cortical area to have an access to multiple sensory modalities to mediate perceptual representation. Studies suggest that the neurons in area V3A (located in BA 19) have distinct neuroanatomical and morphological properties and have neuronal connections with both visual and nonvisual sensory areas of the brain [Zilles and Clarke, 1997]. Functional connectivity of the extrastriate neurons with nonvisual sensory areas is confirmed in human subjects by the neuroimaging studies that have reported extrastriate activity in response to auditory stimuli [e.g., Bookheimer et al., 1998]. Interestingly, stereotaxic coordinates of reduced activity observed in

the present and the earlier studies are close to those of the area V3A [Tootell et al., 1997]. It seems that this area is a key component of the extrastriate perceptual representation system [Badgaiyan et al., 1999, 2000].

The neural mechanism that is associated with priming related reduction in extrastriate activity is unclear. A plausible explanation however comes from the experiments that have recorded single cell activity in the brain of non-human primates. These experiments have observed that a large proportion of neurons in a number of cortical areas show reduced activity when a previously studied stimulus is presented [Baylis and Rolls, 1987; Desimone, 1996]. Because many properties of this “repetition suppression effect” are similar to the behavioral characteristics of perceptual priming, it has been suggested that this effect is responsible for priming-induced reduced activity [Schacter and Badgaiyan, 2000; Wiggs and Martin, 1998].

Interestingly, none of the experiments of conceptual priming has reported reduced activation in the extrastriate cortex. These experiments include visual-to-auditory [Badgaiyan et al., 1999] and auditory-to-visual [Schacter et al., 1999] cross-modality priming, semantic priming [Mummery et al., 1999], semantic number processing [Dehaene et al., 1998], and implicit sequence learning [Rauch et al., 1997]. All of these experiments, however, have reported increased activity in prefrontal cortex suggesting its involvement in conceptual representation [Poldrack et al., 1999].

It is also possible that prefrontal activation observed in conceptual priming experiments may be associated with “executive control” of implicit memory functions [Badgaiyan, 2000]. The prefrontal cortex is believed to exert executive control over conscious cognitive processes [Smith and Jonides, 1999]. Because many of the nonconscious actions involve complex cognitive processing, these actions may also be regulated by an executive control located either in the same cortical area that controls conscious actions or in a different cortical location [for discussion, see Badgaiyan, 2000]. It is worth emphasizing here that the prefrontal activations observed in the present experiment are not associated with priming. These activations were not found in the priming–baseline contrasts and were present in both priming and baseline conditions when the activation patterns were compared with that elicited by look-only conditions. As discussed, these activations may be associated with the cognitive processing that is common to both (priming and baseline) conditions.

Lack of an overlapping pattern of cortical activity in the tasks of perceptual and conceptual priming indicates that perceptual and conceptual representations

are supported by two separate brain systems. Studies on brain-damaged patients further indicate that the two systems are not only independent but are also dissociable. Thus, a lesion in the occipital cortex selectively abolishes a patient’s ability to retrieve perceptual information but not the ability to retrieve conceptual information [Keane et al., 1995; Vaidya et al., 1998].

In spite of the association of extrastriate deactivation with perceptual priming both in the visual and auditory domain, organization of the extrastriate perceptual representation system seems to be modality specific because it is associated with within-modality, and not with cross-modality priming. Thus, using the extrastriate system, a cue could retrieve only those perceptual information that are retained in the same modality. Further, because reduced activation of the extrastriate is observed even when surface features of a cue are different from those of the study items (different voice or different case), it seems that a within-modality cue can access the extrastriate perceptual system even if it has a different surface feature. A change in the feature, however, increases the response time, indicating additional cortical processing, probably to “normalize” the cue by removing surface features.

These observations underscore two characteristics of the extrastriate perceptual system: one, it is easier for the system to recognize a cue if it has similar surface features as the studied item, and two, the system is able to recognize a within-modality cue even if it has a different surface feature. These characteristics suggest that perceptual representation involves two separate groups of neuron. One group (form-specific) retains surface features whereas the other stores a “form-free” representation of a studied item. When a surface feature of a cue matches with that of a studied item, retrieval is accomplished in a single stage by involving both groups of neurons. If features do not match (either in the surface or temporal properties), additional processing is required to remove features. The feature-free cue is then matched with the information retained in form-free neurons. Further, it appears that these neurons maintain modality specificity of stimuli. A cross-modal cue therefore cannot use the extrastriate perceptual representation system.

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