



Short communication

Conscious awareness of retrieval: an exploration of the cortical connectivity

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Abstract

A review of the patterns of brain activation observed in implicit and explicit memory tasks indicates that during conscious retrieval studied items are first retrieved nonconsciously and are retained in a buffer at the extrastriate cortex. It also indicates that the awareness of the retrieved item is made possible by the activation of a reentrant signaling loop between the extrastriate and left prefrontal cortices.

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The purpose of this short report is to propose a new hypothesis concerning cortical connectivity that may be associated with conscious awareness of retrieved information in memory experiments. These experiments have used a number of paradigms to elicit explicit (conscious) and implicit (nonconscious) memory (Schacter et al., 1993). While in the tests of explicit memory subjects consciously recall previously studied items; implicit memory tests are designed to allow retrieval without awareness of

recollection (Graf and Schacter, 1985; Schacter and Badgaiyan, 2001). Interestingly, some of the tests that elicit implicit memory can also be used to elicit explicit memory, if a different set of instructions are used (e.g. word stem completion task). Because in these tests implicit and explicit memory conditions differ only in the set of instructions, and in the presence or absence of awareness, comparison of the patterns of cortical activation elicited in the two conditions could help identify neural networks that may be associated with the awareness of retrieval in memory tasks. Since the word stem completion (WSC) task has been extensively used to elicit both implicit and explicit memory (Badgaiyan and Posner, 1997; Schacter et al., 1996; Squire et al., 1992), this review is focused primarily on the neural events that

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are associated with the processing of this task. In the WSC task, after subjects have studied a list of words, they are shown first three letters (word-stem) of a studied word. To elicit implicit memory, they are asked to complete word stems using the first word that comes to mind. Explicit memory is tested by instructing subjects to complete word-stems using a studied word. Even though, in both conditions studied words are retrieved, subjects typically remain unaware of retrieval in implicit memory condition. Awareness is reported only when they are asked to use a studied word (in explicit memory tasks).

A number of neuroimaging experiments conducted by us and others have identified the brain areas that are involved in the processing of WSC task under implicit or explicit condition (for review see (Schacter and Badgaiyan, 2001)). In addition, we have characterized the temporal attributes of activations using an event related potential (ERP) technique. In the ERP study potentials were recorded over 64 scalp locations while subjects ($n=48$) performed the WSC task under implicit and explicit memory conditions (Badgaiyan and Posner, 1996, 1997). In the implicit memory condition subjects were asked to complete word stems using the first word that came to mind, beginning with the stems. Half of the stems were derived from the study list and the remaining stems came from the words that were not studied. The stems of studied and non-studied words were mixed randomly and presented in a single block. Explicit memory was examined in the same experiment, using similar design but with a different set of instructions. In this condition, subjects were asked to complete word-stems using a studied word. The ERPs obtained in implicit and explicit conditions were averaged across subjects and contrasted against averaged ERPs recorded during completion of the stems of non-studied words (baseline condition).

During implicit retrieval, we observed attenuation of potentials between 64 and 200 ms of stimulus presentation, in the channels located over posterior cortex (Fig. 1). Neuroimaging experiments that have used functional magnetic resonance imaging (fMRI) or positron emission tomography (PET) techniques have also reported reduced activation in the WSC task. These experiments have localized the reduction in the extrastriate cortex (Badgaiyan, 2000; Buckner et al., 1995; Schacter and Badgaiyan, 2001; Squire et

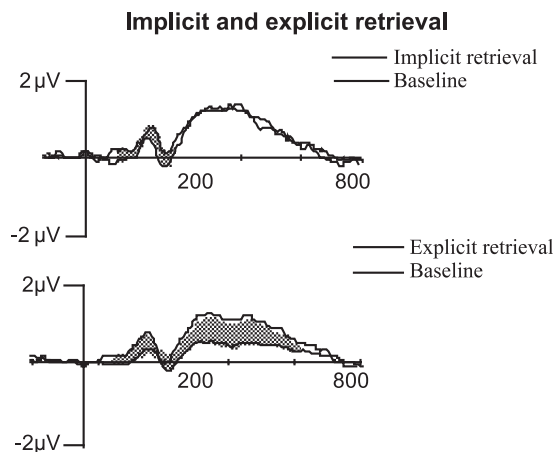


Fig. 1. Grand averaged event-related potentials ($n=48$) recorded during implicit (nonconscious) and explicit (conscious) retrieval of studied words in a word stem completion task. Potentials were attenuated over posterior cortical areas in both conditions in comparison with the baseline condition in which word-stems of novel words were presented. The reduction lasted for ~ 200 ms (early attenuation) during nonconscious retrieval and for an additional 400 ms (late attenuation) during conscious retrieval. Shaded areas indicate statistically significant ($P < 0.01$) differences. The waveforms represent mean potentials across six posterior cortical channels.

al., 1992). Since these experiments have consistently reported significantly reduced activation only in this posterior cortical area, it can be assumed that the generators of the attenuated potentials obtained in the ERP experiment are located in the extrastriate cortex.

It appears that the extrastriate reduction is associated specifically with implicit retrieval. Its association with the visual information processing was excluded by the findings of the auditory priming experiments in which we observed reduced extrastriate activations even though no visual stimulus was used (Badgaiyan et al., 1999, 2001). It also does not appear to be associated with explicit memory mechanisms that are unintentionally activated during performance of some forms of conceptual priming tasks (Schacter and Buckner, 1998). The reductions have been reported in perceptual priming tasks that are not known to elicit explicit retrieval. These tasks include picture priming (Badgaiyan, 2000) and lexical decision tasks (Blaxton et al., 1996). A small area in the extrastriate cortex (area V3A) appears to be particularly interesting in this connection. This area not only has unique morphological and neurochemical properties but also has distinct connectivity. While the

other areas of extrastriate cortex receive most of their input from the visual cortex, area V3A has strong connectivity with the cortical areas that process both visual and nonvisual information.

Even though attenuation of the extrastriate activity has been consistently reported in implicit memory tasks, significance of these attenuations is unclear. We have suggested that it represents the ‘repetition suppression effect’ demonstrated in a number of cortical areas of laboratory animals, when studied items are re-presented (for discussion, see [Badgaiyan, 2000](#)). It appears that during initial presentation of a stimulus, studied items are retained as buffer in the extrastriate cortex. This allows facilitated retrieval that reduces the cognitive load. The attenuation probably reflects this reduction ([Badgaiyan, 2000](#); [Badgaiyan and Posner, 1997](#); [Badgaiyan et al., 2001](#)).

Since subjects are typically unaware of the retrieval in implicit memory tests, the information retained in the extrastriate buffer is not available to conscious awareness. Nonconscious nature of the buffer is suggested also by the studies conducted on blind-sighted patients who have lesions in the primary visual cortex. These patients, despite their inability to see objects in the blind field, are able to nonconsciously identify color, shape, size and movements of objects under forced choice conditions ([Poppel et al., 1973](#); [Weiskrantz, 1997](#)). It has further been shown that their ability of nonconscious detection is lost if the lesion extends to the extrastriate area ([Pasik and Pasik, 1971](#)), indicating that the integrity of this area is essential for retention of nonconsciously acquired information.

Attenuation of the extrastriate activity has been reported not only in the tests of implicit memory but also during explicit retrieval of a studied item in WSC task ([Badgaiyan and Posner, 1997](#); [Buckner et al., 1996](#); [Squire et al., 1992](#)). In the ERP study ([Badgaiyan and Posner, 1997](#)), we found attenuation in the same posterior cortical channels during both, implicit and explicit retrieval of studied items. The attenuation observed during explicit retrieval however, differed with that obtained during implicit memory in its time course. During conscious retrieval, potentials were attenuated between 64 and 600 ms of stimulus presentation, while the reduction in the implicit memory task was observed between 64 and 200 ms ([Fig. 1](#)). It appears that the attenuation during

conscious retrieval occurs in two stages: an early and a late. Since the early attenuation (between 64 and 200 ms) is associated with nonconscious retrieval, the finding is consistent with the idea that the nonconscious retrieval is an inherent component of conscious retrieval in a WSC task ([Squire et al., 1992](#)).

The late attenuation (between 200 and 600 ms) of the extrastriate potentials is an additional activity observed during explicit retrieval. In addition, increased activity in the left frontal area was also observed in the explicit but not in the implicit condition. Neuroimaging experiments that have used WSC task have also reported increased prefrontal activity only during explicit retrieval ([Buckner et al., 1995](#); [Schacter et al., 1996](#); [Squire et al., 1992](#)). Since in the WSC task, the output of explicit retrieval differs with that of the implicit task only in the presence of awareness of retrieval (which was neither needed nor reported in the implicit task), these additional activities might be associated with the processing of awareness, particularly because the time courses of the late extrastriate attenuation and increased left frontal activities are surprisingly similar ([Fig. 2](#)).

Increased activity in different regions of frontal cortex have been reported in a variety of memory tasks including some forms of conceptual implicit memory ([Donaldson et al., 2001](#)). Experiments that have used WSC task however have reported increased prefrontal activation only during explicit retrieval. These activations are generally lateralized on the left hemisphere during attempted retrieval of novel items, and are bilateral during retrieval of studied items ([Badgaiyan and Posner, 1997](#); [Wagner et al., 1998](#)). The left prefrontal activation therefore may be associated with the explicit retrieval of studied words in a WSC task and this part of the frontal cortex may be important for understanding of the neural network involved in the processing of awareness of retrieval.

Because many investigators believe that the frontal cortex is the site most likely to support conscious awareness ([Crick and Koch, 1995](#); [Frith and Dolan, 1996](#); [Goldman-Rakic, 1996](#)), and the extrastriate cortex is the site where the buffer of nonconsciously retrieved information is retained, a communication between the two areas should be essential for the awareness of retrieved information. The association of activities in the frontal cortex with awareness, and that in the extrastriate with nonconscious information

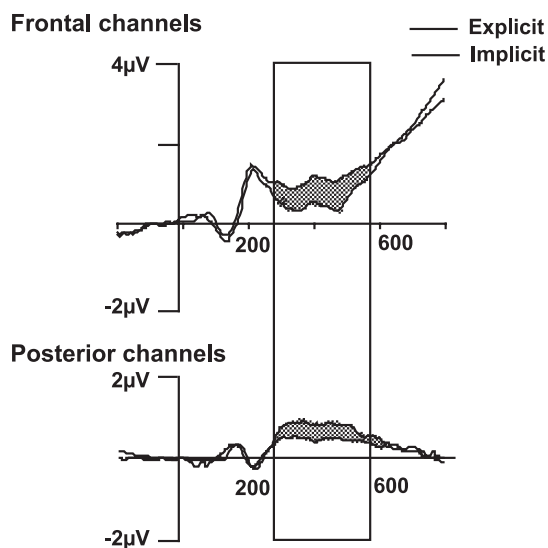


Fig. 2. Comparison of the potentials recorded during implicit and explicit retrieval indicates that the time course of late attenuation (between 200 and 600 ms) observed during conscious retrieval overlaps with the activation in the left frontal cortex. This temporal overlap suggests activation of a reentrant signaling loop between the posterior cortical (extrastriate cortex) and the left frontal cortex. This connectivity may be critical for making implicitly retrieved information available to conscious awareness. Shaded areas indicate statistically significant differences ($P < 0.01$). The waveforms represent mean potentials across five left frontal and six posterior cortical channels.

processing is further supported by the observation in blind-sight patients in which frontal activity is observed only when they are consciously aware of visual events. When the events are perceived non-consciously, there is activity in the extrastriate, instead of frontal cortex (Sahraie et al., 1997). Further, it has been speculated that the frontal cortex and extrastriate play a significant role in the expression of conscious awareness (Crick and Koch, 1995). These areas are significant not only because higher cognitive processing requires effective communication between frontal cortex and the posterior cortical areas that store domain specific information (Goldman-Rakic, 1996; Schacter, 1992), but also because awareness requires construction of a multilevel symbolic interpretation of the information. Neuroanatomical and psychophysical data indicate that such an interpretation can be most effectively performed by the polysensory regions of frontal cortex and extrastriate area (Crick and Koch, 1995).

Analysis of temporal patterns of cortical activity recorded during implicit and explicit memory tasks indicates that during conscious retrieval, a studied item is first retrieved nonconsciously (Squire et al., 1992), eliciting early attenuation of extrastriate potentials. Since the task requires conscious awareness of retrieval, implicitly retrieved information is retained as a buffer for an additional 400 ms (eliciting the late attenuation). During this late attenuation, signals are relayed to the left prefrontal cortex for higher order cognitive processing, eliciting increased activity in this area. Almost perfect overlap of the timing of the late attenuation and the left frontal activity suggests activation of a reverberating circuit making a reentrant signaling loop between these areas (perhaps via intermediate inhibitory interneurons).

Establishment of a reentrant loop is considered essential for conscious awareness by some investigators because the awareness requires appreciation of different qualities of an input signal and such an appreciation can most effectively be accomplished by these loops (Edelman, 1989; Kinsbourne, 1988). Further, our observations suggest that this loop is active for about 400 ms which is consistent with the observations that indicate that a signal can be consciously appreciated only if it stimulates the cortex for about 500 ms (Libet, 1993). The extrastriate–frontal reentrant loop may be the neural mechanism of retaining information in the cortical circuits long enough to allow conscious awareness.

Precise neuroanatomical and neurophysiological characteristics of the extrastriate–frontal loop are unclear. Integration of the temporal and spatial data suggests (as discussed earlier) that it probably connects area V3A and the areas of the left prefrontal cortex that are involved in explicit retrieval. Further, it appears to follow the dorsal stream of occipito-frontal projection which is relayed in the parietal cortex (Baizer et al., 1991). The lesions localized in the dorsal projection, or in the parietal cortex are known to cause disturbances of conscious awareness. For example, patients with damage to the dorsal projection fail to recognize simple geometric shapes (visual form agnosia), but select the slots of correct dimension and orientation when asked to match slots with the wooden blocks of different shapes (Milner and Goodale, 1995), indicating a dissociation between

perception and conscious awareness. A lesion in the posterior parietal area causes another kind of impairment of conscious awareness—the hemineglect. These patients neglect objects located on the contralateral visual fields, despite having the ‘knowledge’ of the presence of these objects (Bisiach and Luzzatti, 1978). Thus, when words and pictures are shown on the neglected fields of parietal patients, despite denying ‘seeing’ anything, they make quicker responses to congruent items presented subsequently to their healthy fields (Berti and Rizzolatti, 1992). The dissociation between perception and awareness observed in these patients could possibly be due to interruption of the parietal relay of the extrastriate–frontal connectivity.

It appears that nonconscious retrieval is driven by the signals that arrive at the extrastriate cortex directly from subcortical structures and not from the primary sensory cortices. In a typical blind sight patient, even though primary visual cortex is damaged, visual signals are nonconsciously ‘perceived’ if the extrastriate cortex is intact, indicating that these signals are not relayed at the primary visual cortex (Stoerig and Cowey, 1997). The data of the ERP experiment also indicate that the extrastriate cortex receives signals from the source other than the primary visual area (Badgaiyan and Posner, 1997). Potential changes in the extrastriate cortex are detected at about the same time (64 ms after stimulus presentation), at which a stimulus is known to activate primary visual cortex (Ikeda et al., 1998).

There is a need to further characterize the nature of the connectivity between the extrastriate and left prefrontal cortex. It will help better understanding of the neurobiology of conscious awareness and may help development of novel therapeutic strategies for the treatment of phenomenon of ‘perception without awareness’ reported in a variety of brain-damaged patients.

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