The effects of visual object priming on brain activation before and after recognition

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Background: Recognizing an object is improved by recent experience with that object even if one cannot recall seeing the object. This perceptual facilitation as a result of previous experience is called priming. In neuroimaging studies, priming is often associated with a decrease in activation in brain regions involved in object recognition. It is thought that this occurs because priming causes a sharpening of object representations which leads to more efficient processing and, consequently, a reduction in neural activity. Recent evidence has suggested, however, that the apparent effect of priming on brain activation may vary as a function of whether the neural activity is measured before or after recognition has taken place.

Results: Using a gradual 'unmasking' technique, we presented primed and non-primed objects to subjects, and measured activation time courses using high-field functional magnetic resonance imaging (fMRI). As the objects were slowly revealed, but before recognition had occurred, activation increased from baseline level to a peak that corresponded in time to the subjects' behavioural recognition responses. The activation peak for primed objects occurred sooner than the peak for non-primed objects, and subjects responded sooner when presented with a primed object than with a non-primed object. During this pre-recognition phase, primed objects produced more activation than non-primed objects. After recognition, activation declined rapidly for both primed and non-primed objects, but now activation was lower for the primed objects.

Conclusions: Priming did not produce a general decrease in activation in the brain regions involved in object recognition but, instead, produced a shift in the time of peak activation that corresponded to the shift in time seen in the subjects' behavioural recognition performance.

Background

The more recently we have seen an object, the easier it is to recognize. This increase in the efficiency with which we recognize recently seen objects occurs even when we cannot recall having seen the object earlier. In other words, there can be an implicit effect on recognition from an earlier presentation of a visual stimulus without any explicit (that is, conscious) recall of that presentation. In the laboratory, this implicit effect of earlier stimulus presentation on later performance is often called priming and has been the subject of extensive behavioural research over the last two decades [1–3].

The fact that priming occurs suggests that simple exposure to a stimulus, say a picture of a common object, somehow changes the efficiency with which the brain processes that stimulus when it is presented again. In the last decade, neuroimaging techniques such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) have been used to determine the

[8,9], a majority of studies using this technique have found an increase in the amplitude of the waveform produced with previously seen stimuli [10–12]. The high temporal resolution of ERPs has permitted investigators to differentiate between activity recorded before and activity recorded after recognition has occurred. Typically, ERP studies have focused on the differences in activity that occur before recognition when primed and non-primed targets are presented. Neuroimaging studies, with their low temporal resolution, are unable to differentiate between these different stages of recognition and the technique simply blurs the pre- and post-recognition activation. Indeed, in most cases, the target is still present long after recognition has occurred and, thus, the observed activation may be reflecting mostly post-recognition processes. The one enormous advantage that neuroimaging has over ERP methods, however, is high spatial resolution. ERPs may provide information about the time course of activity during the recognition of a primed stimulus, but very little information about where that activity originates.

What is needed then is a way of separately examining pre- and post-recognition processing of primed stimuli using neuroimaging. One way to do this is to use a method of presentation in which the target stimulus is gradually revealed or uncovered, thus prolonging the time required to recognize the stimulus. Such a method of presentation allows one to measure the sub-components and time course of visual recognition that are usually masked by the rapidity with which recognition occurs. Gradual presentation techniques have been used extensively to study object recognition in normal and patient populations [13–16]. In a preliminary experiment [17], we used this technique in combination with high-field fMRI to study possible differences in the patterns of activation that occur during object recognition in more detail. The results of this experiment showed a clear difference in the level of activation produced by primed and non-primed objects after recognition had taken place, with the non-primed objects producing more activation than primed objects, a result that was consistent with the earlier imaging literature. There was a suggestion, however, that in the period before recognition quite the opposite pattern had occurred, although this result was not as compelling as the post-recognition difference. Although we had not predicted this result, if the activation in the pre-recognition phase were indeed higher for primed objects than non-primed objects, then this result, like the ERP experiments discussed earlier [10–12], would challenge the idea that priming always produces a suppression of brain activation [3]. To pursue this possibility in the present study, we improved the gradual presentation technique by using higher-quality images and two different kinds of masking. This more powerful design allowed us to look more closely at the pre-recognition phase of the activation time course and to compare quite directly the characteristics of individual time courses with the recognition performance of each subject. We anticipated that, again, non-primed objects would show more activation during the post-recognition phase but we also expected that primed objects would show more activation during the pre-recognition phase.

Results

We first identified those regions of the brain that were selectively activated when subjects viewed a set of the objects that we used to study priming. We compared the patterns of activation produced in subjects' brains when they viewed grey-scale images of common three-dimensional objects with the patterns of activation produced when they simply looked at a fixation point presented on a homogeneous dark background. This subtraction revealed large areas of bilateral activation in the posterior cortex and a single region of bilateral activation in the frontal cortex. Three main foci of activation were identified in the posterior region: the peri-striate region (PS), which included visual areas V2 and VP [18], the fusiform region (FG), which included regions of the fusiform gyrus within the temporal and occipital lobes, and an area in the posterior parietal cortex (PP; Figure 1). The single site of activation identified in the frontal region was in the dorsolateral frontal cortex (DLF) at the junction of Brodmann's areas 9 and 44. All three of the posterior sites have been shown to be involved in the visual processing of objects. The FG is important for recognition of shape [19–24], whereas the areas of the PS perform a lower-level visual analysis of the stimulus. The PP is involved in processing spatial relationships within a stimulus [25–27]. A separate experiment confirmed that the location of the FG was the same as that of the lateral occipital complex [28] as defined by a comparison of objects and scrambled objects. The DLF has been associated with the processes underlying object memory [29,30].

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the subjects using one of two gradual presentation tasks. In one condition, the objects were revealed from behind six vertically oriented virtual panels; in the other condition, they were revealed from behind a random noise mask (Figure 2). During each stimulus presentation, which lasted for 61 seconds (the time it took to acquire 24 functional images at 2.56 seconds per image), the subject indicated when they recognized an object by pressing a button. The criterion for recognition was that subjects could name the object (silently). As expected, speed of recognition was faster for the primed than the non-primed objects for both tasks ($F_{(1,13)} = 10.9$, $p < 0.01$). Subjects who completed the noise task did not perform as well as did subjects who completed the panel task ($F_{(1,13)} = 9.1$, $p < 0.01$). There was, however, no interaction between task and priming, indicating that the priming effect was of the same magnitude in both tasks (Figure 3a).

Time courses from the functional data collected during the data shown in Figure 4 were analyzed after collapsing across both tasks.

During the post-recognition period (that is, after the subjects had pressed the button), significantly greater activation was obtained with non-primed as opposed to primed stimuli in all four brain regions (Figure 4; grey area, $p < 0.05$). During the pre-recognition phase, however, greater activation was observed with the primed stimuli, but this difference was significant only in the FG and PP (Figure 4; yellow area, $p < 0.05$). As Figure 4 makes clear, the pattern of differences (higher activation for the primed stimuli in pre-recognition and higher activation for the non-primed stimuli in post-recognition) appears to be due to a leftward shift in the peak of the activation curve for primed stimuli, accompanied by no shift in the amplitude of this peak.

also separately within the primed and non-primed objects ($r_{(13)} = 0.47$, $t_{(13)} = 2.65$, $p < 0.01$; $r_{(13)} = 0.65$, $t_{(13)} = 2.05$, $p < 0.05$). These data appear to indicate that faster recognition, whether due to previous experience with the object or to an easier recognition task, was related to a words, activation that reflected processes that were occurring long after recognition had taken place. Any activation that might reflect processes leading up to recognition was simply swamped because recognition took place so rapidly.

recognition, we found that activation declined sharply. One might speculate that this decline in activation is related to the task demands. Before recognition, the subject is actively processing the stimulus in an attempt to identify it. After recognition, such active processing would no longer be required — even though the stimulus is still present on the screen. Thus, the decline in activation could reflect a decrease in the overall arousal of the system, a decrease in the level of motivation of the subject or, most likely, a decrease in the amount of selective attention dedicated to processing the stimulus. Whatever the explanation might be, it appears that the processes that are responsible for the decline in activation after recognition has occurred are only indirectly related to previous experience with the stimulus.

Conclusions

Although data collected under gradual presentation conditions may not generalize completely to situations involving rapid presentation, this method has provided new data were collapsed (Figure 4), standardization for the primed and non-primed trials was carried out using the mean recognition time across subjects and tasks. This interpolation algorithm was implemented using Matlab™ software.

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