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.

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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 characteristics of those changes [3–7]. In general, these experiments have found that, when subjects are again shown visual stimuli they have just seen, less activation is observed in the occipitotemporal cortex as compared with the activation observed in these same areas when the subjects are shown new visual stimuli. This decrease in neural activity, which is evident in areas implicated in object recognition, has been interpreted as reflecting a selective reduction in the number of neural units necessary for coding the stimulus. This sparser, but more efficient, coding is thought to lead to faster recognition [3].

One problem with this model is that it is based on data derived from PET or fMRI techniques that have temporal resolution that is several orders of magnitude lower than the time required to recognize a visual stimulus. Researchers using other methods that have much higher temporal resolution, such as event-related potentials (ERP), have findings that appear to stand in marked contrast to the neuroimaging results. With very few exceptions

[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].

In addition to providing information about the location of areas involved in object recognition, this initial phase of the experiment was used to prime the subjects with a set of visual stimuli that the subject would encounter again in a later phase of the experiment. Each of these stimuli (plus a set that was not used again) was presented ten times to the subjects to also allow us to establish the presence of the typical priming effect by comparing activation during the first and last presentations. When this comparison was carried out, we observed more activation in the FG, PP and DLF during the first stimulus presentation than during the last presentation (Figure 1). This reduction in activation, particularly in the FG, replicated the findings of previous neuroimaging studies, including a recent study that found a reduction in all the areas reported here [31].

In the second phase of the experiment, the primed objects (and an equal number of new objects) were presented to
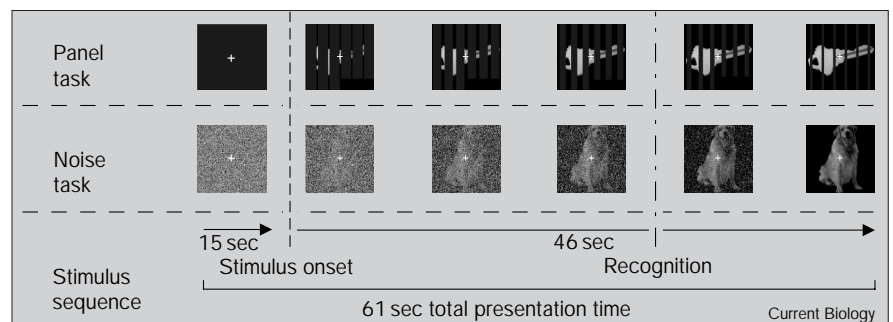
Figure 1
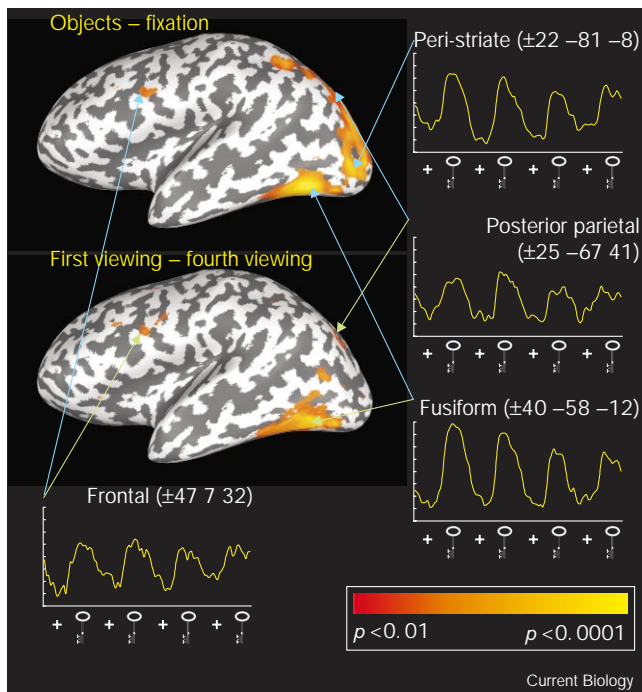
Localization of brain regions involved in object processing. The two brain images are inflated representations of the lateral view of the left hemisphere. Dark grey regions indicate sulci and light grey regions indicate gyri. The activation map in the upper brain image was generated by comparing periods of object viewing with periods of fixation. Thus, the peaks of the time courses occurred during periods of object viewing (indicated by the key symbol), and troughs in the time courses occurred during periods of fixation (indicated by the cross symbol). Because the same group of objects was presented repeatedly, an activation map showing regions that produced a reduction in signal to repeated presentations of a stimulus (that is, a priming effect) could also be calculated. The lower brain image shows a comparison of the first and last presentations of the group of objects (that is, the first and fourth peaks in the time courses). Levels of significance (*p* values) for the activation maps are corrected for multiple comparisons. The horizontal axes represent functional images collected in time. The vertical axes represent signal strength. Talairach co-ordinates [35] for each of the four regions are given after the name of the region (x y z). All regions showed bilateral representation.

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 gradual presentation tasks were plotted (Figure 4) for each of the four brain regions described in Figure 1. The curves shown in Figure 4 were fit to the data to characterize possible differences in the overall shapes of the activation time courses for primed and non-primed stimuli. To obtain these curves, we performed separate cubic polynomial regression analyses on these time courses. For all brain regions, the best fit to the data for the non-primed stimuli was achieved with a third-order coefficient that did not differ significantly from zero ($t_{(13)} = -0.85$, not significant). In contrast, the best fit to the data for the primed stimuli was provided by a third-order coefficient that was significantly greater than zero ($t_{(13)} = 3.38$, $p < 0.005$). This was true whether the fit was performed separately on the panel task data or the noise task data or on an averaged data set. Figure 5 illustrates this difference in the activation functions across tasks for the FG region. The first- and second-order coefficients also showed differences between the primed and non-primed data, and again these differences were the same for both presentation tasks (first: $F_{(1,12)} = 0.036$, not significant; second: $F_{(1,12)} = 0.032$, not significant). Therefore, because there was no interaction between priming and task for any of the coefficients,

Figure 2

The gradual presentation protocol. Objects were gradually revealed over a 46 sec period, during which the subject responded with a button press at the same time that they silently named the object. The presentation of each stimulus was preceded by 15 sec of baseline fixation for a total presentation time of 61 sec per object. In the panel task, virtual panels gradually shrunk to reveal the object, whereas in the noise task, randomly determined pixels of noise were gradually removed to reveal the object.

(a) Recognition

(b) Peak activation

(c)
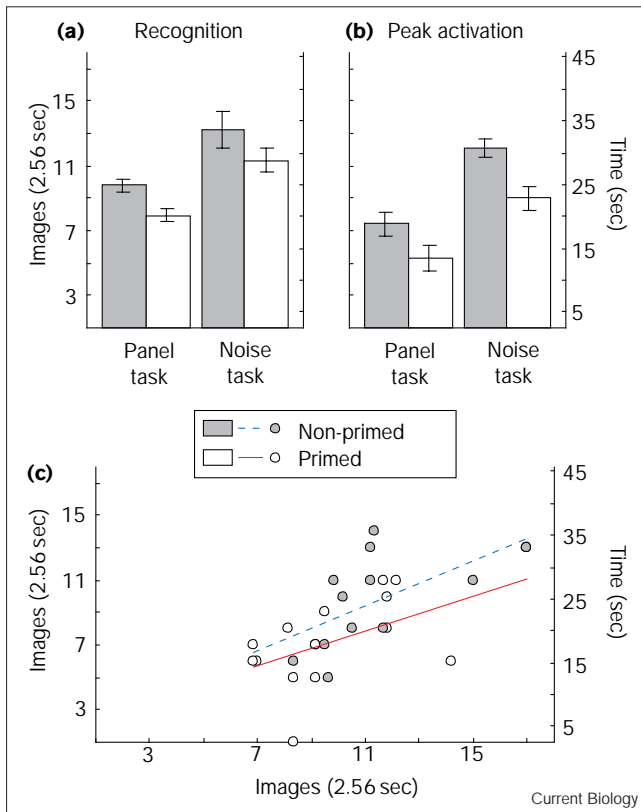
Figure 3

(a) Recognition times as a function of task and priming condition. The primed objects were recognized faster than the non-primed objects whether the objects were revealed from behind virtual panels or from behind a mask of noise. The horizontal axis indicates the two different tasks that subjects performed. The two vertical axes both represent time, with the right axis measured in seconds and the left axis measured in number of functional images collected (at 2.56 sec each). **(b)** Peak activation times as a function of task and priming condition. Activation for the primed objects peaked sooner than activation for the non-primed objects whether the objects were revealed from behind virtual panels or from behind a mask of noise. Axes are the same scale as in (a). **(c)** Recognition times as a function of peak activation time. Data points represent individual subjects. Lines were fit to the primed or non-primed data separately. Time of recognition and time of peak activation were significantly correlated for primed and for non-primed objects.

(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.

Figure 3b illustrates the time of peak FG activation measured for primed and non-primed objects for each task. The pattern of results is similar to the recognition-time data shown in Figure 3a, that is, primed peaks occurred sooner than non-primed peaks ($F_{(1,12)} = 5.42$, $p < 0.05$) and panel task peaks occurred sooner than noise task peaks ($F_{(1,12)} = 22.8$, $p < .001$). Figure 3c illustrates a similar point, but with individual subject data. Behavioral recognition times were plotted against peak activation times for each subject for either primed or non-primed objects. Not only was there a significant correlation across primed and non-primed objects ($r_{(27)} = 0.64$, $t_{(27)} = 2.95$, $p < 0.01$), but

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

Activation time courses with primed and non-primed objects for each brain region. Yellow bars, periods before recognition of the object when the primed and the non-primed time courses were significantly different from each other ($p < 0.05$); grey bars, periods after recognition of the object when the primed and the non-primed time courses were significantly different from each other ($p < 0.05$); red and blue vertical lines, the average time of recognition (as measured behaviorally) for the primed and the non-primed objects, respectively. Each data point is the combined data of 14 subjects viewing six different objects. The curves are cubic polynomial functions fitted to these data. Across regions, the third-order coefficient was not different from zero for the non-primed time
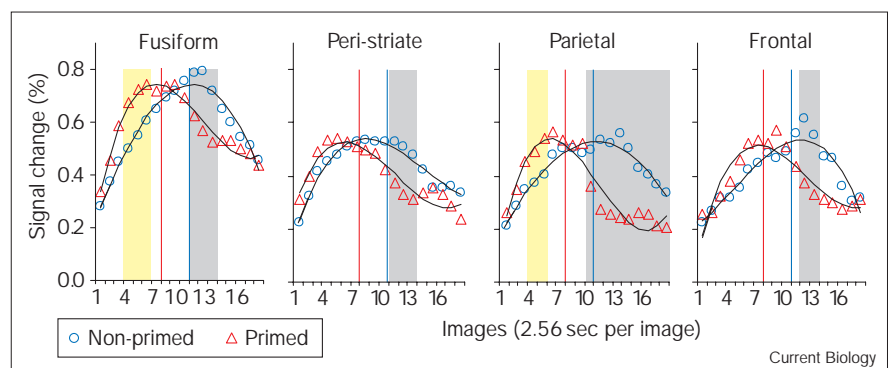
courses, but was greater than zero for the primed time courses. The horizontal axis represents the number of functional images

(2.56 sec each) that were collected. The vertical axis represents percent signal change above baseline.

Figure 5
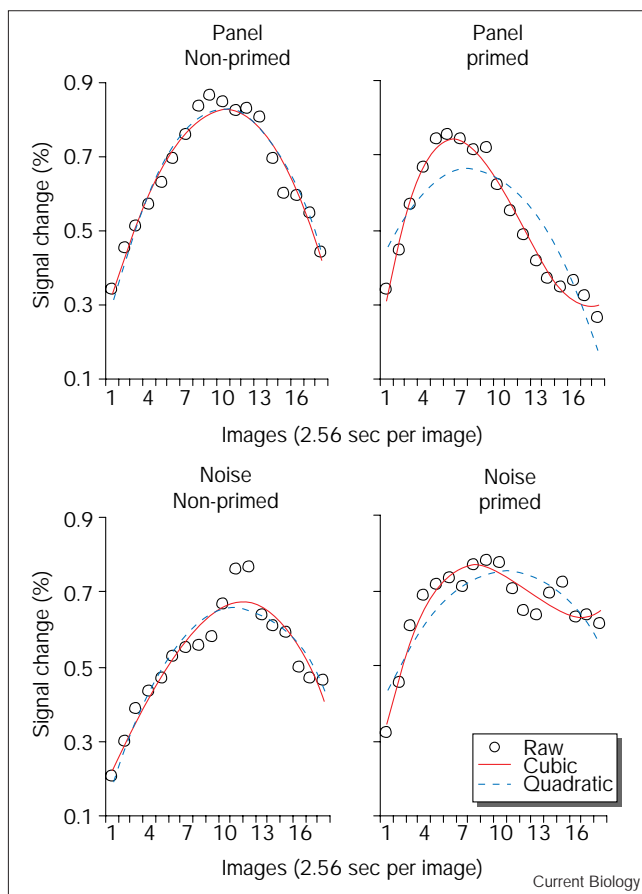
Activation time courses from the FG region for primed and non-primed objects for the panel and noise tasks. Each data point is the combined data of seven subjects viewing six different objects. Cubic and quadratic polynomial functions were fitted to each set of data. For the non-primed objects (left two graphs), the cubic and quadratic curves appeared to be the same, that is, the third-order coefficient in the cubic fit did not differ from zero. For the primed objects (right two graphs), however, the cubic and quadratic curves appeared different. This was because the third-order coefficient in the cubic fit was significantly greater than zero. These differences in the fit of the cubic and quadratic functions occurred regardless of whether objects were revealed from behind virtual panels or a mask of noise. The horizontal axis represents the number of functional images (2.56 sec each) that were collected. The vertical axis represents percent signal change above baseline.

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 faster rise to peak activation.

Discussion

In this experiment, objects were slowly revealed to subjects while their brains were scanned using high-field fMRI. By gradually revealing the hidden object, we were able to slow down the process of recognition and thus study in more detail the changes in activation that occurred in different brain areas before and after the point of recognition. We used this technique to examine changes in the levels of activation that occurred before and after recognition for primed and non-primed objects. We tracked these changes in activation in four brain regions that we identified as being implicated in visual object processing: the FG, a region in the PP, the DLF, and areas in the PS.

In the FG, the level of activation increased gradually from the time of stimulus onset (when the object was just beginning to be revealed) and reached a peak level at the time of recognition (when more of the object was visible). The fact that a highly degraded, unrecognizable image of an object would produce less activation in this region than a less degraded, recognizable image of the same object has been shown before [21]. After recognition, however, the level of activation decreased rapidly, even though the stimulus remained present on the screen and continued to be revealed until it was completely visible in the noise task and almost (85%) completely visible in the panel task. As is evident in Figure 4, the same general pattern of changing activation was seen not only in the FG, but also in the PP, a region in the DLF and, to a lesser extent, in areas of the PS. The activation patterns observed in these regions, in which activity increased to a peak at recognition and then rapidly declined, are not easily explained as the action of a single mechanism. Moreover, the fact that priming had differential effects on the level of activation in the pre- and the post-recognition periods suggests that something more complex must have been occurring.

During the post-recognition period, less activation was observed with primed than with non-primed objects in all four regions we examined. This lower activation with primed stimuli in the post-recognition period mirrored the effect that was observed during the first phase of our experiment, in which a set of stimuli was repeatedly presented but each stimulus was on the screen for only 1 second. During that phase, activation was higher in the occipitotemporal cortex, particularly in the FG, for the initial presentation of the stimuli as compared with a later presentation of those same stimuli. In other words, once the subject had been primed with a particular object, the level of activation for that object was lower when it was presented again — a result that is consistent with previous studies of priming [3,5]. Two other regions, one in the PP and one in the DLF also showed a drop in activation after repeated presentations of the stimuli. Lower activation in these areas, as well as in the FG, have also been reported in two recent studies of priming [4,31]. Taken together, these findings suggest that most studies of priming that have used standard imaging methods and short presentations of the primed and non-primed stimuli were measuring activation from the post-recognition period — in other

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.

Our method of gradual presentation allowed us to look at what happened to levels of activation before recognition took place. Contrary to what the earlier neuroimaging studies might have predicted, we found that, during the pre-recognition period, primed objects generated more activation than non-primed objects, just the opposite to what we found in the post-recognition period. This difference was most clear-cut in the FG, an area that has been implicated in object recognition, but was also evident in the PP. The higher level of activation with primed objects during pre-recognition (and the reversal of this pattern in the post-recognition period) appears to be related to the fact that peak activation occurred earlier in the time course for primed as opposed to non-primed objects. In short, there was a steeper rise in activation in the FG and PP for the primed objects, but the actual amplitude of the peak activation for primed and non-primed objects did not differ. This difference in the slopes of the time courses for primed and non-primed objects again suggests that the activation in the pre-recognition period was not a simple reflection of bottom-up, stimulus-driven processes. Furthermore, those models that suggest that priming involves a functional 'pruning' of a population of neurons [3], and thus less activation on subsequent presentations, cannot easily account for the increase in activation before recognition. Whether the observed pre-recognition increase in activation reflects top-down influences or some change in local circuitry remains an open question. In any case, this pre-recognition difference in the activation associated with primed and non-primed stimuli that occurs before conscious recognition of the object must reflect the operation of implicit processes.

The increase in activation with primed stimuli that occurred before the point of recognition in our study is similar to that observed in studies that have used ERPs to measure brain activity. Like our method of gradual presentation in fMRI, the use of ERPs allows investigators to look at differences in brain activity that might occur before recognition. Traditional fMRI studies, on the other hand, do not have sufficient temporal resolution to do this. In most fMRI studies, activation is measured by summing across entire recognition events. As pointed out above, any differences that might be present before recognition would be masked by differences in activation after recognition, in which processes not directly related to recognition would be reflected in the activation. Thus, if the post-recognition period in the neuroimaging studies was of the same length or longer than the pre-recognition period, then it is likely that a decrease in activation to primed stimuli would be observed. In fact, in most of

these studies, the stimuli were on the screen for at least 2 seconds (some as long as 4 seconds), a period of time that is much longer than would be needed for recognition. Thus, it is fair to say that most of the differences in activation recorded in neuroimaging studies to date have been measuring signal differences that occurred well after the point of recognition.

There are some reports in the imaging literature that previous experience with a stimulus results in higher activation when the same stimulus is presented again. On the surface, these reports appear to corroborate our finding that priming produces an increase in activation prior to recognition. Two of these studies [27,32] measured activation to degraded images of objects (either through blurring or contrast polarity reversal), both before and after the presentation of the non-degraded images of the same objects. Activation to the degraded images after presentation of their non-degraded counterparts was higher than before. Another study [33] measured activation across repeated presentations of novel sets of stimuli. As the stimuli became more familiar, activation increased. One problem with interpreting these results in the context of the current priming experiment is that these studies confounded recognition with familiarity. During the first presentation of a stimulus, subjects were often unable to recognize it, but as they became more familiar with that stimulus, recognition was more likely. Thus, as familiarity increased, so did the probability of recognition. But it is known that the FG region responds better to stimuli that are recognizable than those that are not, even when other low-level visual factors are kept constant [21–23]. Thus, in the studies described above, the increase in brain activation with a particular group of stimuli could have been due to either familiarity (priming) or to an increase in the probability of recognition. In our study, however, subjects were able to recognize every stimulus, with some stimuli taking longer to recognize than others. Indeed, because our experimental paradigm involved the gradual unmasking of a target stimulus, the probability of recognition across priming conditions was not a factor.

In the present experiment, we found that the level of activation increased as the stimulus was gradually unmasked for both primed and non-primed stimuli. Presumably, this increase in activation is related to the amount of information or evidence that can be extracted from the image and used to make a decision about its identity. One might speculate that previous experience with a stimulus facilitates this evidence-gathering period of the recognition task, possibly through feedback from higher-level areas, although, as mentioned earlier, we cannot rule out that it is through changes at the local level. The resulting interplay between bottom-up signal processing and top-down modulation from stored experiences could increase pre-recognition activation in regions such as area FG. After

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 insights into how visual object priming affects brain activation. By 'slowing down' the process of recognition in this admittedly artificial way, we have revealed a striking correspondence between psychological events and abrupt changes in brain activation. In short, the act of recognition is reflected by a peak in the time course of activation in areas of the brain implicated in object processing. Moreover, priming affects brain activation in these areas well before subjects have recognized an object and these effects are quite different from those that occur after recognition.

Materials and methods

Subjects
The subjects were 16 graduate students (10 women and 6 men) attending the University of Western Ontario. Ages ranged from 23 to 32 years with a mean age of 26.5 years. Subjects were all right-handed, had normal or corrected-to-normal visual acuity and had no history of neurological disorder. Two subjects were excluded from the analyses because of uncharacteristic behavioral and functional data profiles. This left 14 subjects in total, seven of whom completed the panel task and the other seven the noise task.

Object stimuli
All stimuli were greyscale images of common three-dimensional objects. Images were rear-projected onto a screen and viewed through a mirror placed within the head coil. Total viewing distance was 60 cm and the principle axis of all objects subtended ~6° of visual angle. The subjects were instructed to fixate on a cross in the center of the screen throughout all tasks.

Passive object viewing
Stimuli were presented one at a time, for 1 sec each in completely random order and were selected from a group of six objects that the subject would be tested on later (primes) and a group on which they would not be tested (distracters). Presentation alternated between 30 sec periods of object presentation and 30 sec periods of fixation. This sequence was repeated four times, resulting in each object (distracters and primes) being presented an average of 10 times (10 sec).

Gradual presentation tasks
A schematic of the two gradual presentation tasks is shown in Figure 2. The presentation of each object began with 15 sec of baseline followed by 46 sec of gradual revealing of the image (61 sec total). Subjects were instructed to fixate on a white cross in the center of the screen and press a button when they were able to recognize the object. It was explained to the subjects that their criterion for recognition should be that they could name the object (silently). The subjects were discouraged from responding according to whether or not they felt they had 'seen the object before'. They were encouraged to maintain a constant level of confidence about their recognition judgements. After the button press, the object continued to be gradually revealed while the subject viewed it. Twelve objects were used for each task, six primed and six non-primed, counterbalanced across subjects. Although the subjects were instructed at the beginning of the session that they would have to recognize both primed and non-primed objects, on individual trials they were unaware of whether a primed or a non-primed object would be shown. Object trials were run in three separate 4 min scans for each task in order to reduce subject fatigue.

For the panel task, gradual revealing was accomplished by 'superimposing' six vertically oriented virtual panels over the object and then shrinking the width of the panels continuously until 85% of the object was showing. For the noise task, gradual revealing was accomplished by masking the object with greyscale noise and then removing noise pixels from random locations on the image continuously over time until 100% of the object was showing. Eighty-five percent revealing was used in the panel task because pilot testing showed that it was easier than the noise task.

Scanning parameters
All imaging was done using a 4 Tesla, whole-body MRI system (Varian; Siemens) and a quadrature head coil. The field of view was $22.0 \times 22.0 \times 8.5$ cm, with an in-plane resolution of 64×64 pixels and 17 contiguous axial scan planes per volume, resulting in a voxel size of $3.4 \times 3.4 \times 5.0$ mm. Images were collected using a T2*-weighted, segmented (navigator-corrected), interleaved EPI acquisition (TE = 15 msec, TR = 640 msec, flip angle = 45°, 4 segments per plane) for blood oxygen level dependent (BOLD) [34] based imaging. Each volume (17 planes) required 2.56 sec to acquire. Functional activation data were superimposed onto high-resolution T1-weighted anatomical images (three-dimensional magnetization-prepared (MP) turbo FLASH acquisition using an inversion time (TI) of 500 msec (TE = 6 msec, TR = 11 msec, flip = 11°)).

Data analysis
Functional data were analyzed using Brain Voyager™ software. All functional images underwent two-dimensional motion correction and temporal and spatial band-pass filtering (full-width half-maximum of 2 pixels) before being transformed into the stereotaxic space of Talairach and Tournoux [35]. The regions described in Figure 1 were defined by comparing the object viewing and fixation states from the data collected during passive object viewing using the General Linear Model. Time courses from individual object trials were then extracted from individual subject's functional data that were acquired during the gradual presentation tasks. Because the recognition times were different for each trial, time courses from individual trials were standardized to the mean recognition times across subjects and/or tasks for the primed and non-primed objects. That is, pre- and post-recognition portions of the time courses of individual trials were expanded or compressed so the point of stimulus onset, the time of the button press, and the end of the trial were aligned across trials. Note that we did not standardize the curves on the basis of the time at which peak activation occurred, but instead on a known behavioral marker, the time at which subjects pressed the button to indicate recognition of the object. When individual trials for each subject were analyzed (Figure 3b,c), primed and non-primed trials were standardized separately using that subject's mean recognition time (that is, button-press time) for the primed and non-primed trials. When the panel task and noise task data were analyzed separately (Figure 5), standardization for the primed and non-primed trials was carried out using the mean recognition time across subjects for each task. Finally, when the panel and noise task

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.

Acknowledgements

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