WE investigated the effects of repetition priming on the time course of recognition in several visual areas of the brain using fMRI. We slowed down recognition by gradually revealing the stimuli, in order to prolong the pre-recognition phase. Activation was lower for primed than for non-primed objects overall in both the occipitotemporal region (OTR) and the intraparietal region (IPR). A difference was found between primed and non-primed objects in the rate of increase of OTR activation. We concluded that the IPR, in addition to the OTR, was affected by repetition priming, and that this effect was different from that seen in the OTR. *NeuroReport* 10:1019–1023 © 1999 Lippincott Williams & Wilkins.

Repetition priming and the time course of object recognition: an fMRI study

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Introduction

Objects that we encounter regularly are more easily recognized than objects that are less familiar. This difference in behavior is reflected in the activity of high-level visual areas of the primate brain, particularly in the ventral (or perceptual) stream of cortical visual processing, that projects from area V1 to the temporal cortex [1]. Thus, the response of single units in the inferior temporal cortex (IT) of the monkey is reduced with repeated presentations of the same visual stimulus; a phenomenon called repetition suppression [2]. In humans, event-related potentials (ERPs) recorded from the occipitotemporal region also show a reduced response to repeated (or primed) stimuli [3]. The advent of functional neuroimaging (PET and fMRI) has resulted in a number of studies showing that repetition priming [4] leads to a reduction of activity in the ventral stream, particularly the region surrounding the occipitotemporal junction [5–7].

Because ERPs and single unit responses are recorded at a much higher temporal resolution than either fMRI or PET, these techniques provide a more detailed look at the profile of functional brain activation. Both ERP and single unit studies have found that responses to primed and non-primed stimuli begin to differ before any overt response occurred [3,8]. Despite its poor temporal resolution, fMRI provides much higher spatial resolution than do ERPs. In the present study, we took advantage of the high spatial specificity of fMRI to study where in the visual pathways the effects of object priming occurred, but at the same time we used a new paradigm that allowed us to examine the time course of object recognition. We made it difficult for participants to recognize objects quickly by revealing the objects only gradually over time, thereby making high temporal resolution unnecessary. We predicted that activation to primed objects would be lower than activation to non-primed objects in high-level visual areas of the ventral stream. We also predicted that differences would begin to appear before an overt response occurred.

Materials and Methods

Participants were all graduate students attending the University of Western Ontario, were right-handed, spoke English as their first language, and had no history of neuropsychological disorder. There were eight participants in total, four men and four women, with ages ranging from 22 to 27 years.

All imaging was performed with a 4 T, whole body MRI system (Varian, Palo Alto, USA; Siemens, Erlangen, Germany) and a quadrature head coil. The field of view was $19.2 \times 19.2 \times 5.0$ cm, with an in-plane resolution of 64×64 pixels and 10 contiguous scan planes per volume, resulting in a voxel size of $3 \times 3 \times 5$ (mm). Slices were oriented perpendicular to the calcarine sulcus and spanned from the occipital pole to the posterior aspect of the

corpus collosum. Images were collected using a T2*-weighted, segmented (navigator corrected), interleaved EPI acquisition (TE = 15 ms, TR = 500 ms, flip angle = 45°, four segments/plane) for BOLD-based imaging [9]. Each volume (10 planes) required 2.0 s to acquire. Functional activation data were superimposed onto high-resolution T1-weighted anatomical images (3D magnetization prepared (MP) turbo FLASH acquisition using an inversion time (TI) of 500 ms; TE = 6 ms, TR = 11 ms, flip = 11°).

Participants were placed within the magnet in a supine position, with their head firmly supported by foam padding within the RF coil. Participants viewed a rear projection screen though a mirror within the coil. The screen was placed such that it straddled the participant's waist and was 60 cm from the mirror. Images were projected onto the rear projection screen using an NEC LCD projector. The maximum viewing area of the screen was 20° horizontal by 15° vertical.

Checkerboard viewing: To help distinguish between areas of the brain that were processing low-level and high-level object information, we used two different stimuli to determine regions of interest (ROIs) in our images, a checkerboard stimulus and an object stimulus (described below). We used a circular checkerboard stimulus that was contrast reversing, flickered at 8 Hz and subtended 15° of visual angle. The checkerboard was presented to participants for 24 s, followed by a black screen for 24 s, while the participant fixated a central cross. This sequence was repeated three times.

Passive object viewing: This phase of the experiment served two purposes. First, it allowed us to identify voxels in our images that were involved in processing objects. Second, it allowed us to pre-expose the participants to specific objects before the recognition phase of the experiment. In this way, we were able to prime some of the objects and not others. Objects were presented in the center of the screen one at a time for 2 s each, resulting in 24 s of object presentation. Each presentation of the series of objects (see Fig. 2A) was followed by a 24 s period during which only a homogeneous grey screen was shown to the participant. This sequence was repeated four times, resulting in each object (distracters and primes) being presented four times. Participants were informed before the experiment began that some of these objects would be used later in the recognition experiment and that they should study them in order to make the objects easier to recognize later. Participants were instructed to fixate on a cross in the center of the screen throughout.

Gradual presentation task: A schematic of this task is shown in Fig. 1C. The presentation of each object began with 12 s of baseline, a homogeneous grey screen with a fixation cross in the center. The object then began to be revealed, as if from behind vertical venetian blinds that were opening slowly. This was accomplished by superimposing six vertically oriented virtual panels over the object and gradually shrinking the width of the panels. The object was revealed over a 48s period, at the conclusion of which, 80% of the object was showing. Participants
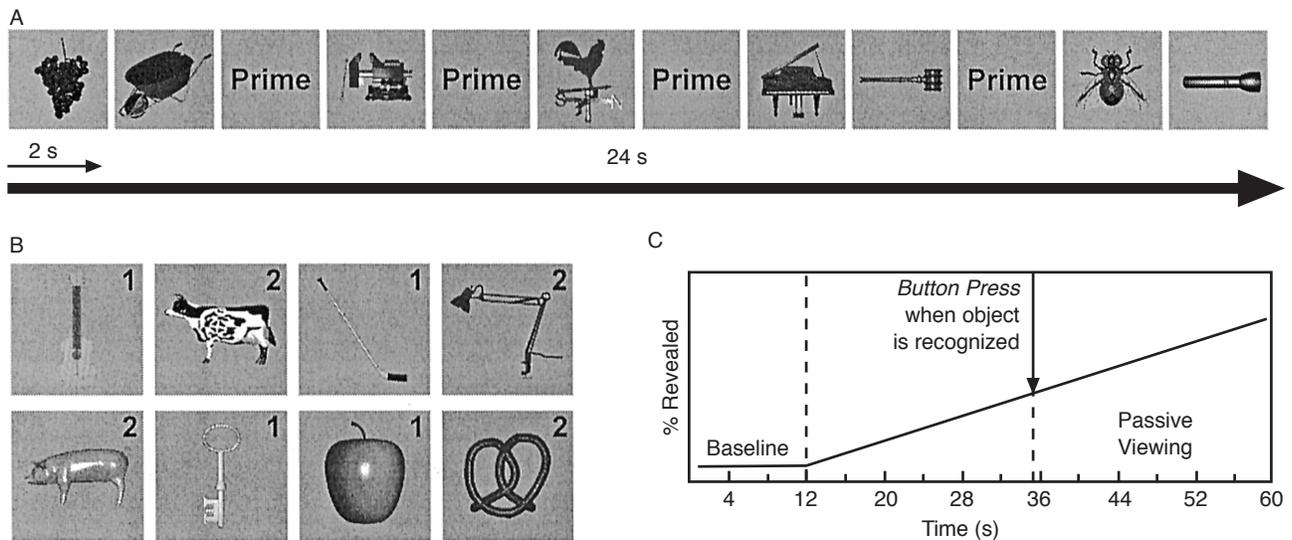

FIG. 1. (**A**) Objects used during passive object viewing. Each object was presented for 2 s in the sequence indicated. Four primes, chosen from (**B**), were presented along with the distracters. B) Objects used during the gradual presentation task. Objects were in two groups and for each participant, only one group of four objects was presented during passive object viewing as primes. (**C**) A schematic of the gradual presentation task. Twelve seconds of baseline was followed by the object being gradually revealed over a 48 s period until 80% of the object was showing. Participants pressed a button when recognition occurred and these times were recorded. All objects were greyscale, rendered views of familiar, nameable objects. The long axis of each object subtended 8–10° of visual angle.

were instructed to fixate on a cross in the center of the screen, and press a button when they recognized the object. After the participant pressed the button, the object continued to be revealed while the participant continued to view it. In this way, each object trial required 60 s (12 s baseline, 48 s of object presentation) to complete. These trials were run in two 4 minute blocks. The eight objects that were used for these trials, and the order that they were presented in, are shown in Fig. 1B.

All of the functional imaging data were analyzed using Stimulate [10] software. Regions of interest (ROIs) were determined for each participant individually by analyzing the data from the checkerboard and passive object viewing phases of the experiment. A cross-correlation technique [11] was used to find voxels in the images that responded significantly more to the stimulus state (checkerboard or objects) than to the homogeneous grey state. All voxels had to meet at least two criteria to be included in an activation map, a minimum correlation coefficient value of $r = 0.30$, and that it be a member of a cluster of contiguous voxels of a size not less than six [12]. These criteria produced an effective significance level per voxel between $p < 0.002$ and $p < 0.02$.

Functional images that were collected during the gradual presentation task were analyzed for excessive motion by creating animation loops and center-of-intensity profiles. None of the eight participants produced sufficient motion artifacts to warrant exclusion from further analyses. Time courses were then extracted from voxels within the ROIs. These data were converted into percent signal change scores, using the average signal intensity of the four baseline conditions within each run to establish a baseline level. Time courses were then normalized (using interpolation), setting recognition time for each trial to the averaged recognition time for primed or non-primed objects. Performing this normalization allowed comparisons of the pre- and post-recognition periods across participants and objects.

Results

The early visual ROI (EVR) was defined on the checkerboard activation map. Voxels were included in this ROI if they were within the grey matter surrounding the calcarine sulcus in the two most posterior, consecutive slices that showed activation. This procedure for defining early visual areas assumed the inclusion of areas V1 and V2 in the ROI [13,14]. The occipitotemporal ROI (OTR) was defined on the object activation map. Voxels were included in this ROI if they were within the fusiform or inferior temporal gyri or the collateral

sulcus, all areas that have been shown to be involved in the high-level processes underlying object recognition [15-21]. The voxels also had to be in the three most anterior, consecutive slices that showed activation. The intraparietal ROI (IPR) was also defined on the object activation map. Seven of eight participants showed one or more foci of activation along the intraparietal sulcus, though there was considerable individual variation in terms of where along the sulcus the activation occurred. Parietal activation during object recognition has been described in several studies [18,20,21], and is most likely associated with the processing of metric information about objects [1,22].

The averaged primed and non-primed time courses for the OTR are shown in Fig. 2. Time courses from the other two ROIs were similar. Averaging the signal across pre- and post-recognition phases showed significant differences between the primed and non-primed conditions in the OTR ($t(7) = 1.90$, $p < 0.05$) and the IPR ($t(7) = 3.08$, $p < 0.01$), with a non-significant trend in the EVR ($t(7) = 1.73$, $p < 0.1$).

We then analyzed the pre-recognition data points in isolation, in order to determine if the activation functions were different for the primed and non-primed objects. Regression lines were fitted to the pre-recognition data points for each participant and then the slopes were compared. There was a significant difference between the primed and non-primed slopes of the time courses extracted from the OTR (Fig. 3), but not from the IPR or EVR. The signal increased more rapidly in the primed condition than in the non-primed condition in the OTR ($t(7) = 2.06$, $p < 0.05$).

Peak activations for primed and non-primed objects were also analyzed. The peak activation for each participant was determined as the maximum
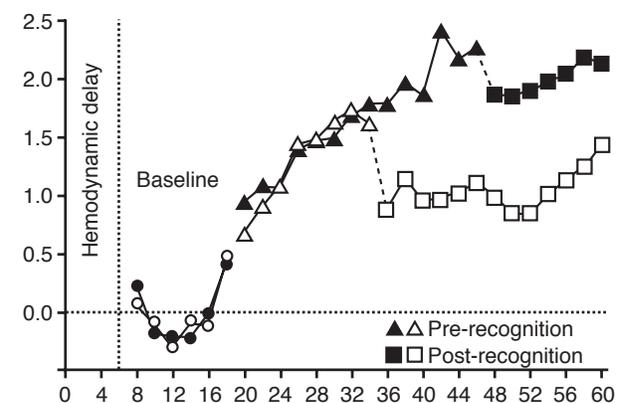

FIG. 2. Percentage signal change as a function of time for the occipito-temporal region (OTR). Participants recognized the primed objects ($M = 34.5$ s, $s = 2.2$) significantly sooner than the non-primed objects ($M = 46.0$ s, $s = 1.8$; $t(7) = 2.7$, $p < 0.05$). Symbols: filled = non-primed, hollow = primed.
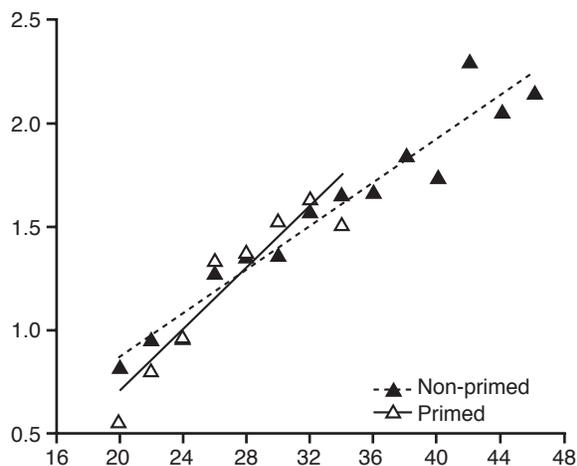
FIG. 3.   Percentage signal change as a function of time for pre-recognition data points from the occipitotemporal region (OTR). The primed signal increased more rapidly than the non-primed signal.

value of each time course averaged across trials. Peak activation was significantly lower for the primed than for the non-primed objects in the OTR ($t(7) = 2.36$, $p < 0.03$) and IPR ($t(7) = 2.07$, $p < 0.05$), but not in the EVR. The OTR difference can be observed in Fig. 2, where the peak for the primed objects occurred at 32 s and the peak for the non-primed objects occurred at 42 s. In both the primed and non-primed conditions, the peak activation occurred just prior to the time of the recognition response.

Discussion

By gradually revealing the visual stimuli, we were able to increase the time that it took participants to recognize the stimuli. Combining the use of fMRI with this method of presentation allowed us to examine the process of object recognition with higher spatial and temporal resolution than has been possible before. In particular, it allowed us to examine whether there was a difference in activation to primed (previously viewed) and non-primed objects during the 'pre-recognition' period (before the participants indicated they had recognized the stimulus) in three ROIs, the EVR, OTR and the IPR.

Overall, the level of activation in the OTR was lower for primed than for non-primed objects. This finding replicates the results of other studies of repetition priming that have found lower activation levels in ventral stream structures with primed stimuli, even though these earlier studies used short stimulus presentation times [5–7]. However, we also found that overall activity in the IPR was lower for primed than for non-primed stimuli. To our knowledge, an effect of repetition priming has never been

reported in this posterior parietal (PP) area, even though studies have utilized many different types of stimuli [5–7]. It has been suggested that recognition of a degraded image of an object may require the recruitment of structures in PP cortex that are involved in spatial reconstruction and feature binding [23]. In the present experiment, spatial reconstruction could have been facilitated by prior exposure to the non-degraded object, resulting in reduced activation in the IPR.

As can be seen in Fig. 2, the overall differences just described were due mostly to large post-recognition differences between primed and non-primed signals. This would have been the portion of the time course that was measured in most other neuroimaging studies of repetition priming. The present data showed that the non-primed signal continued to climb while the primed signal dropped (at 34 s). Thus, past studies of repetition priming could have reported differences in activation that were due simply to faster recognition times for the primed stimuli. The present data showed that the pattern of activation was different between primed and non-primed stimuli. Even after recognition of non-primed stimuli occurred, the signal did not drop to the level of the primed stimuli.

The levels of activation observed in EVR did not differ significantly between primed and non-primed visual stimuli, and this was true for all the measures that we used. The absence of any effect of repetition priming on the activity of early visual areas was consistent with many other studies that have looked at activity in primary visual cortex (for review see [5]). Nevertheless, there was a hint that overall activity might be lower with primed objects and it is possible that a more detailed analysis will reveal subtle effects of priming on early visual areas. Certainly, slowing down the whole recognition process, as we did in this study, offers a way of examining this possibility.

The differences in fMRI signal to primed and non-primed stimuli in the OTR and IPR were also seen in peak activation, which was lower for primed stimuli. From other functional imaging studies, we know that primed stimuli produce less activation on average than non-primed stimuli [5–7]. We also know that primed objects are recognized faster than non-primed objects [4,24] and our study was no exception. Taken together, these results could be interpreted as meaning that primed stimuli require a lower level of activation for recognition to occur if primed and non-primed objects have the same rate of increase of activation in the period leading up to recognition. The pattern of activation observed in the IPR is consistent with this explanation; in other words, the level of activation achieved before recog-

nition occurred with the primed objects was lower than for non-primed objects, but the rates of increase of activation during the pre-recognition phase were the same.

Although peak activation was lower in the OTR for primed stimuli, it appears that this was not the only factor that influenced faster recognition of primed as opposed to non-primed stimuli. Activation in the OTR increased more rapidly for primed objects than for non-primed objects after stimulus onset. Thus, even if (hypothetically) the same level of activation was required for the recognition of primed and non-primed stimuli, recognition would still have occurred sooner if the rate of increase of activation was greater for primed stimuli. In short, mechanisms in the OTR that participate in the more rapid recognition of primed stimuli may do so by virtue of a combination of an elevated rate of increase in activation and a lower threshold of required activation.

Conclusions

We analyzed the time course of recognition for primed (previously viewed) and non-primed objects by slowing down recognition by gradually revealing the stimuli. Primed objects produced less activation than non-primed objects in the occipitotemporal region, an area implicated in processing the perceptual properties of stimuli in order to determine identity. Primed objects also produced less activation in the intraparietal region, an area implicated in the spatial reconstruction of degraded images. Activation in the occipitotemporal region increased at a faster rate for primed objects than for non-primed

objects prior to recognition, a difference in the pattern of activation that was not seen in the intraparietal region. This new paradigm for studying the effects of prior experience on object recognition not only allows us to identify regions that show differences in activation before recognition takes place, but also allows us to chart differences in the pattern of activation observed in these different regions across the entire time course of recognition.

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