Neural correlates of change detection and change blindness

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Functional magnetic resonance imaging (fMRI) of subjects attempting to detect a visual change occurring during a screen flicker was used to distinguish the neural correlates of change detection from those of change blindness. Change detection resulted in enhanced activity in the parietal and right dorsolateral prefrontal cortex as well as category-selective regions of the extrastriate visual cortex (for example, fusiform gyrus for changing faces). Although change blindness resulted in some extrastriate activity, the dorsal activations were clearly absent. These results demonstrate the importance of parietal and dorsolateral frontal activations for conscious detection of changes in properties coded in the ventral visual pathway, and thus suggest a key involvement of dorsal–ventral interactions in visual awareness.

Detecting change in the visual environment is of considerable evolutionary importance, yet research has shown that people are remarkably poor at detecting a change if it occurs during a brief visual disruption, such as a screen flicker[1,2]. Under normal circumstances, abrupt changes in the visual environment involve sensory transients easily detected by early visual areas in the brain. However, the visual disruption ('flicker') used in change-blindness experiments[1] effectively masks those transients, resulting in blindness for surprisingly large changes that are obvious once attention is drawn to them (for example, an entire jet engine disappearing from an airplane scene).

Because the flicker method can result in either change detection or change blindness for the very same stimulus, it provides a powerful but as yet unused probe for the neural correlates of visual awareness of change. Comparing trials in which subjects consciously detect a change to trials in which they are blind to it should reveal activity due to processes involved in awareness of the change. In contrast, comparing trials in which subjects are unaware of the change to trials in which no change is present should reveal stimulus-driven but unconscious processing of change.

Using event-related fMRI, we examined which neural systems are active when subjects consciously detect a visual change versus when they are functionally blind to an equivalent change. Subjects were asked to detect changes in either of two peripherally presented visual images while simultaneously engaging in a primary letter detection task (Fig. 1). The primary letter task served two purposes. First, it ensured that subjects maintained fixation on the center of the display. Subjects had to monitor for the presence of an X in one of two letter strings positioned 2.4° of visual angle above and below fixation. These small letters could not be resolved if subjects made an eye movement away from the center. The primary letter task also provided a means to titrate subjects' performance on the change detection task. It has long been known that dividing attention between two tasks typically produces a performance cost in the secondary task that varies with the difficulty of the primary task[3]. In this case, we varied the difficulty of the primary letter detection task per individual so that each subject produced approximately equal numbers of detections and misses in the secondary change detection task.

Changes in two different image categories were investigated: faces and outdoor scenes (or 'places'). These image categories were chosen because they selectively activate different regions of the ventral visual pathway[4–6]. We could thus distinguish between activity related to change detection in general and activity related to the detection of the particular type of changing object. One quarter of all trials were no-change trials, in which the images remained the same between sequential displays.

Results

Experiment 1

Performance on the primary letter task was close to ceiling (95% correct target detections and 9% false alarms), suggesting successful maintenance of fixation. Moreover, performance on the primary letter task did not vary as a function of whether subjects detected the change (95%) or failed to detect the change (94%), confirming that central fixation was maintained regardless of whether subjects detected the change or not. In addition, performance on the change detection task was no better on trials in which the target letter was absent (change detection rate, 41%) than on trials in which the target letter was present (change detection rate, 51%), suggesting that subjects did not make eye movements to the change detection task when the target was absent in the primary letter task. The opposite trend, for somewhat worse performance on the target absent (versus present) trials, is typical of visual search tasks. Finally, varying the difficulty of the primary letter task was successful in producing an equivalent rate of change detections and misses. Average detection rate was 48% for faces and 53% for places.

Functional MRI scans from six participants were submitted to a fixed effect analysis to identify brain areas where activity

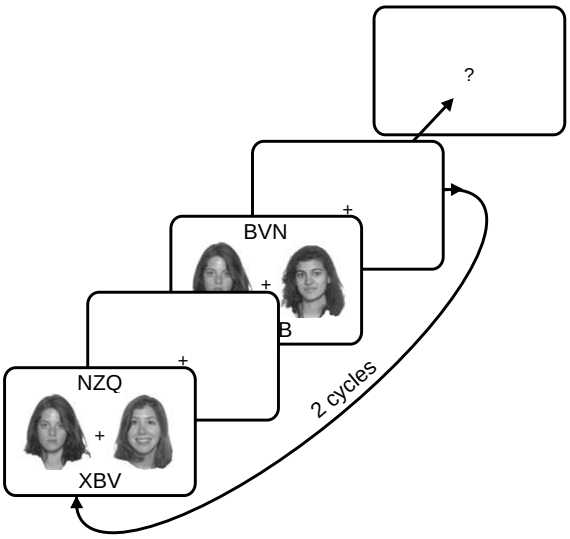

Fig. 1. Face change trial. Subjects received two cycles of the displays shown before receiving the display with a question mark, resulting in a total of four image displays (separated by fixation blanks). Once the question mark appeared, subjects had two seconds to respond as to whether or not a change occurred.

was consistently related to conscious change detection. We first compared detected and undetected change trials. Because the task and stimuli are identical, activity revealed by this comparison must be related to cognitive processes involved in awareness of the change. Areas activated involved both the visual ventral stream and frontoparietal cortex. Activity related to detected changes diverged within the ventral stream according to the type of image detected (Fig. 2a). Conscious detection of face changes resulted in increased activity in areas of the fusiform gyrus previously associated with face perception[4,5], whereas conscious detection of place changes resulted in activity in a more medial and anterior region of the fusiform gyrus, a region that is near but posterior to the 'parahippocampal place area' previously reported[6]. In contrast to the divergent face versus place activity in the ventral stream, detection-related activity for face and place changes converged in the dorsal stream and frontal lobes (Fig. 2b).

Regardless of whether changes occurred to faces or places, three main sites were activated by detected change relative to undetected change (Fig. 3): fusiform gyrus (encompassing both place and face sites), bilateral parietal lobe, and the right dorsolateral prefrontal cortex (BA 46). (See Table 1 for coordinates and *t* values.) We next established the degree of overlap (using a masking procedure) between the detected and undetected change contrasts for faces and places. This analysis revealed that activity common to both face and place conscious change detection involved only the parietal and dorsolateral prefrontal cortex, but none of the ventral areas. Thus, in contrast to the traditional account of the ventral and dorsal streams' roles in awareness, on which the ventral pathway is described as 'conscious' and the dorsal pathway as 'unconscious'[7], our results emphasize the importance of dorsal activations for awareness and suggest that awareness depends on joint activation of dorsal frontoparietal structures and category-specific regions of the ventral stream.

Next, we compared trials in which subjects did not detect a change versus the no-change trials. Because the stimuli are different but subjects' perception is the same, differential activity revealed by this comparison reflects stimulus-driven unconscious processing of change. In contrast to conscious change detection, we found much less activation during change blindness, consistent with subjects' reports of not seeing a change. Only three significant regions of activity were identified for undetected changing faces, and none for places. Specifically, there was significant activation of an area in the fusiform gyrus superior and anterior to the activation for consciously detected face changes, plus the lingual gyrus and the inferior frontal gyrus (Table 1). These activations suggest that the ventral stream processed and in some sense 'detected' the change, but that activation of these ventral loci alone (that is, in the absence of associated dorsal activity) was not sufficient to evoke awareness. As there was no overlap between the areas of activity related to conscious change detection versus change blindness, it is unlikely that the activity for change blindness merely represents low-confidence conscious detec-

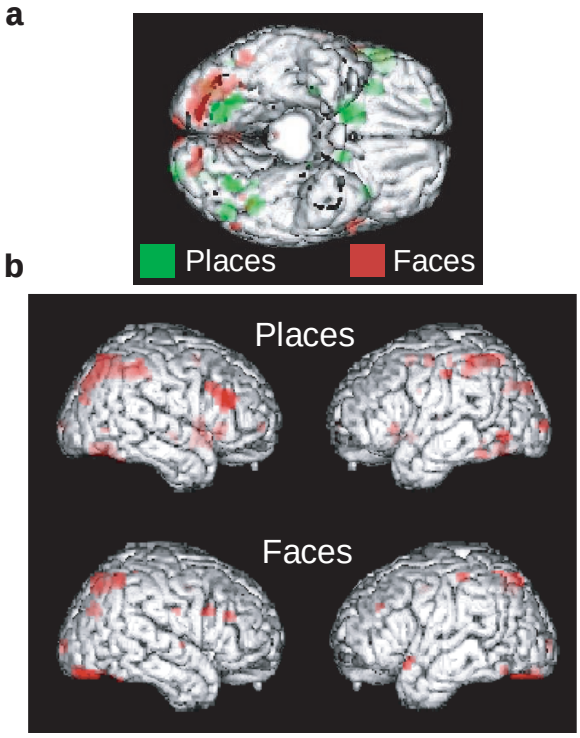

Fig. 2. Activity related to category-specific conscious detection of change. (**a**) An inferior view of a T1-weighted anatomical template brain upon which are superimposed loci where evoked activity was greater during consciously detected change compared to undetected change. Activity is superimposed in red for faces and green for places. At the corrected threshold of $p < 0.05$, the peak locus of activation for face change detection was at Talairach coordinates 36, –78, –21 ($t = 5.17$), and at 18, –69, –15 ($t = 4.21$) for places. A statistical threshold of $z = 3.09$ ($p < 0.001$, uncorrected) was used for display purposes. Even at this lower threshold, areas activated by detected face and place changes remain distinct. (**b**) Left and right lateral views of the same comparison as in (**a**), with loci of activation superimposed in red for both faces and places. The similarity of the frontal and parietal activations for face changes and place changes contrasts strongly with the distinct ventral stream activations shown in (**a**).

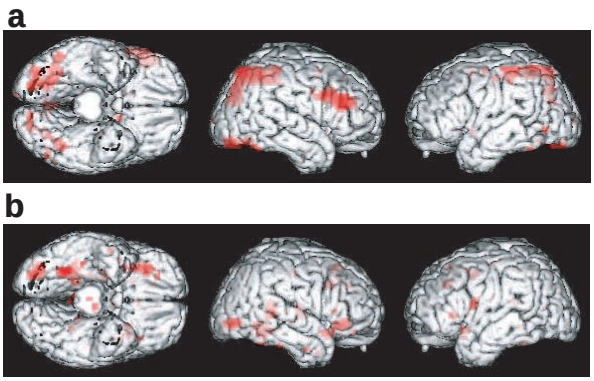

Fig. 3. Results from experiment 1 shown on three views of the T1-weighted anatomical template. (**a**) Activity related to conscious change detection (detected > undetected), pooled across stimulus category. (**b**) Stimulus-driven activity related to change blindness (undetected > no change) for faces only. Places did not produce any significant activity in this comparison. The statistical threshold is the same as in Fig. 2.

tion. The finding that faces produced some activation during change blindness whereas places did not suggests that the visual system may be particularly sensitive to changes in faces[8], producing a stronger stimulus-driven activity for them.

Taken together, our results demonstrate a strong association between dorsal activity and the visual awareness of properties coded in the ventral stream. Although conscious detection of change evoked activity in both dorsal and ventral streams, some ventral stream activity was also found in situations of change blindness. However, dorsal activity in the parietal lobes and dorsolateral prefrontal cortex was associated exclusively with the conscious detection of change.

Experiment 2

Our observation that frontoparietal activation was associated with conscious change detection raises the possibility of an unwanted contribution from eye movements, as these areas are involved in eye movement control. As we have argued earlier, the high degree of accuracy on the primary letter detection task found in both detected and undetected change trials suggests that fixation remained central. Nevertheless, it seemed important to determine conclusively that the frontoparietal activation we found cannot be attributed to eye movements. In a second experiment, we therefore replicated the experimental and imaging parameters of the first experiment, while monitoring eye movements during scanning in four additional subjects.

Behavioral findings closely paralleled those in the first experiment. As before, subjects' performance on the primary letter task was close to ceiling (98% correct target detections and 6% false alarms), and did not vary as a function of whether subjects detected the change (98%) or failed to detect the change (97%). The average change detection rate was somewhat higher than in experiment 1, with subjects detecting 56% of the face changes and 59% of the place changes. As in experiment 1, performance of the change detection task was no better on trials in which the target letter was absent (change detection rate, 49%) than on trials in which the target letter was present (change detection rate, 57%).

No difference was seen in eye position comparing detected and undetected change trials. Eye position was calculated during detected and undetected trials in 100-ms bins, to detect the effects of quick saccades on eye position as well as slow drifts. A frequency histogram of eye position in all subjects for all detected and undetected change trials confirmed that fixation was well maintained, and that there was no difference in eye position between the trial types (Fig. 4). Thus, differential brain activity comparing detected and undetected change trials cannot be attributed to eye movements.

The functional MRI scans from the four participants were submitted to the same fixed effect analysis as those of the first six participants. As can be seen in Fig. 5, the imaging results of this experiment were very similar to those of experiment 1. Detected change relative to undetected change was associated with activity in the fusiform gyrus, the parietal lobes and a region of right dorsolateral prefrontal cortex slightly anterior to that found in experiment 1. This replicates our original findings, confirming that frontoparietal activation is associated with conscious change detection, and showing that eye movements cannot account for this activity. The comparison of undetected versus no change revealed no significant activity.

The replication of our experimental method afforded the opportunity to conduct a random effects analysis, combining the imaging data from all subjects in experiments 1 and 2 (n = 10). Such an analysis is more statistically conservative, but can allow generalization of our findings beyond the study population. Comparison of detected versus undetected change revealed highly significant foci of activation in both ventral stream and bilateral parietal cortex (Table 2; Fig. 5). The fact that conscious detection of change resulted in the joint activation of the parietal cortex and category-specific areas of the ventral stream in this random effects analysis reflects the consistency of this activation across subjects (Fig. 5). Differential prefrontal activation was not seen in this new analysis, which may reflect the conservative nature of the random effects analysis or, alternatively, the variation in location of prefrontal activation seen when comparing the two experiments.

The comparison of undetected change versus no change using the random effects model yielded no significant activity. This is not surprising, given the weak activation in experiment 1 and the absence of any significant activity in this comparison in exper-

Table 1. Experiment 1 results: brain regions associated with conscious change detection and change blindness.

Brain region	Hemisphere	Cluster size (voxels)	*x*	y	z	*t* value
Change detection (detected > undetected)						
Parietal lobe	R/L	871	–24	–60	60	5.43
Dorsolateral prefrontal cortex	R	247	51	30	24	5.88
Fusiform gyrus	R	225	36	–60	–27	4.71
Change blindness (face: undetected > no change)						
Lingual gyrus	R	65	30	–78	–3	4.26
Fusiform gyrus	R	137	33	–51	–12	3.97
Inferior frontal gyrus	R	75	33	33	–6	4.15

Only clusters with a significant activity of $p < 0.05$ corrected for multiple comparisons are reported.

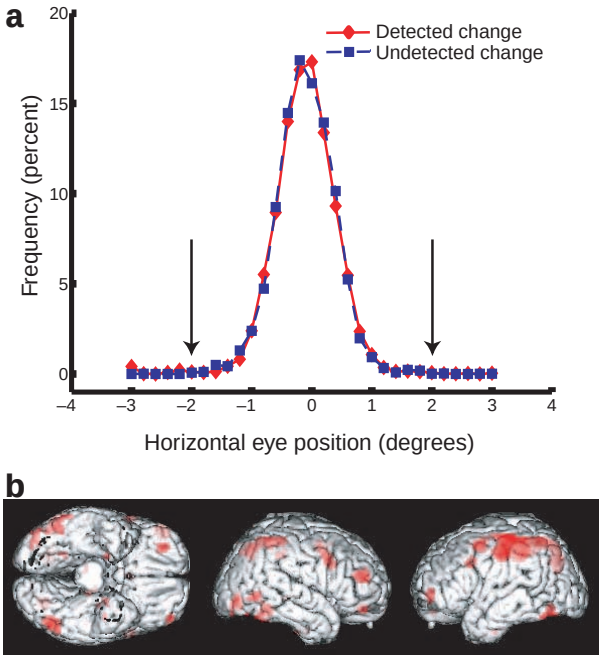

Fig. 4. Results from experiment 2. (**a**) Frequency histograms of horizontal eye position across all subjects for detected and undetected change trials. Mean eye position was calculated over 100-ms intervals during all portions of a trial in which an image was on the screen. (**b**) Activity related to conscious detection of change (detected > undetected), pooled across stimulus category. The anatomical template and statistical threshold are the same as in Fig. 2.

iment 2. The overall absence of significant activity in this comparison is consistent with subjects' reports of 'change blindness.'

Discussion

Our data suggest that joint activation of category-specific regions in the ventral stream and the parietal regions of the dorsal pathway is crucial for visual awareness of change. Previous neuroimaging and neurophysiological studies of awareness[9–11] have concentrated on the role of the ventral stream and have not typically considered the potential role of dorsal stream activations. Indeed, the higher levels of the ventral visual pathway are good candidates for some aspects of visual awareness because there is abundant evidence that these regions are selective for specific stimulus categories[4–6,12]. Moreover, lesions to these areas can give rise to corresponding category-specific deficits in awareness[13].

Although our conclusion that the dorsal pathway is crucial to awareness stands in sharp contrast to traditional accounts that suggest an exclusive role for the ventral stream in visual awareness[7], it allows us to integrate a wide range of previously disparate neuropsychological and neuroimaging findings. Despite an intact ventral stream, lesions to the parietal lobe may result in unilateral neglect, which is characterized by a lack of awareness of stimuli in the contralesional visual field[14,15]. Moreover, parietal regions are active during conscious perceptual transitions in binocular rivalry[16] and while viewing bistable visual figures[17]. Activity in a dorsal area, including the intraparietal sulcus, correlated with awareness in a study focusing on the correlation of ventral stream activity with recognition performance[10]. More recently, frontoparietal activation was found to be associated with detection as well as correct rejection of a coherent motion stimulus[18]. Thus, although there have been some previous hints of the involvement of parietal structures in visual awareness, until now, the evidence for this has been sparse or has come from rare neurological syndromes and anomalous situations produced by bistable perception. Our experiment confirms dorsal/prefrontal involvement in visual awareness for normal observers in the fundamental task of change detection.

The two most common functions associated with the frontoparietal network are eye movements and selective attention[19,20]. Having ruled out eye movements as a potential confound, we suggest that selective attention is important in awareness. There is abundant evidence that selective attention determines the extent to which a stimulus is processed[21–23] and that attention determines the inclusion as well as exclusion of information from perceptual awareness[24,25]. Moreover, the importance of attention in change detection is consistent with studies demonstrating that the phenomenon of change blindness is not reducible to visual masking (induced by the global blanking in the flicker method), but can also be found during the simultaneous appearance of additional objects[2] and in real-world interactions[26]. In all cases, what seems to be critical for change blindness is that attention is deployed elsewhere when the change occurs. Further evidence for the role of attention in change blindness comes from the findings that changes in objects of central interest, or those likely to draw attention, are detected much sooner than other changes[1,2,8]. All these reports suggest that attention plays a causal role in the detection of change. Specifically, it is proposed that attention is needed to code the identity of objects across time[1].

Indeed, our method of using the dual task technique to divide attention between the change detection task and a primary letter detection task suggests a causal role for attention in change detection. Varying the difficulty in the primary letter task invariably determined the accuracy of detection in the secondary change detection task. Although these behavioral measures demonstrate a causal role for attention in the conscious detection of change, our imaging study is not informative regarding the exact nature of the relationship between attention and awareness. Our studies clearly establish an anatomical association between dorsal parietal regions that are related to attention and awareness-related activation of category-selective areas of the ventral stream. This association suggests either that conscious detection requires previous allocation of attention to the changing images, or that attention is drawn to the change after it is detected. The latter pos-

Table 2. Random effects analysis: brain regions associated with conscious change detection.

Brain region	Hemisphere	Cluster size (voxels)	*x*	y	z	*t* value
Change detection (detected > undetected)						
Parietal lobe	L	135	–30	–42	48	12.08
Parietal lobe	R	119	42	–51	51	10.84
Fusiform gyrus	R	43	30	–45	–15	8.15

Only clusters with a significant activity of $p < 0.05$ corrected for multiple comparisons are reported.

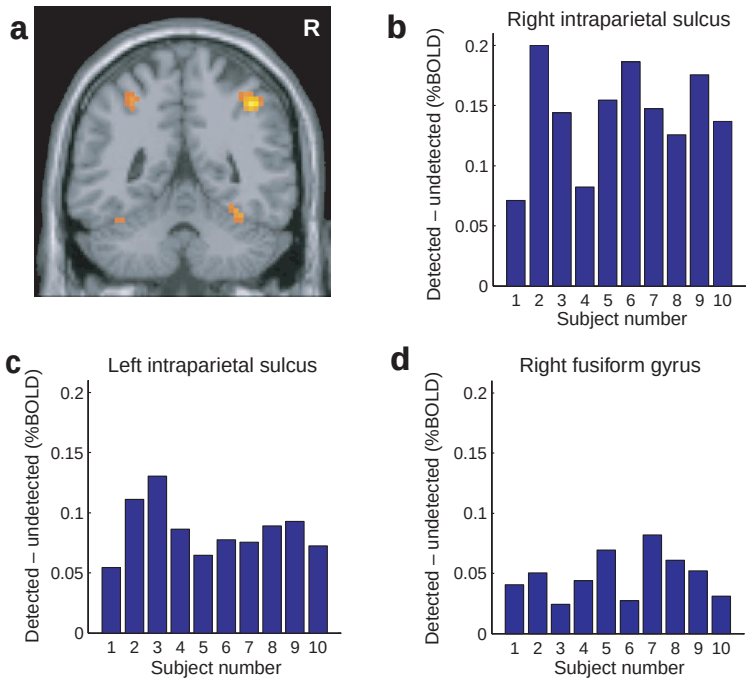

Fig. 5. Results of the random effects analysis of the 10 subjects in experiments 1 and 2. (**a**) A coronal slice (y = –48) through an anatomical template brain in the stereotaxic space of Talairach and Tournoux, upon which are superimposed loci that showed significantly greater activation for detected change trials than undetected change trials. Prominent activation in bilateral intraparietal sulcus and right fusiform gyrus is apparent. For display purposes, the statistical threshold is set at $p < 0.001$ uncorrected, but these loci reached a statistical threshold of $p < 0.05$, corrected for multiple comparisons. (**b–d**) Activation that contributed to the composite picture in (**a**) is plotted separately for each of the cortical area in each of the 10 subjects. Shown is the mean difference in BOLD contrast (units in percent BOLD contrast relative to the global mean) comparing detected and undetected change trials. Activity is taken from the voxel of peak activation (coordinates displayed in **Table 2**) in (**b**) right intraparietal sulcus (**c**) left intraparietal sulcus and (**d**) right fusiform gyrus. All subjects show differential activation in all areas comparing conscious detection with undetected changes; the level of activation is qualitatively highest in right IPS and higher in parietal areas than in the fusiform gyrus.

sibility may still indicate a causal role for attention in allowing for a perceptual event to reach awareness. For example, we found face-specific activity in the ventral stream when subjects were blind to the change, indicating that the brain, in some sense, registered the change. However, ventral activity resulted in awareness only when found jointly with parietal activity. Perhaps, then, full awareness requires both ventral activation (typically associated with object perception) and parietal activation (typically associated with attention). These issues should be resolved by further study.

For the moment, we conclude that conscious detection of visual changes relies not only on regions of the ventral visual cortex specialized for the visual category that changed, but also on the parietal and, to some extent, on the prefrontal cortex. Although previous research on visual awareness has typically emphasized the ventral visual pathway to the exclusion of the dorsal pathway, our data suggest that visual awareness is the result of an interaction of the ventral and dorsal streams.

Methods

Subjects. Informed consent was obtained from 6 subjects in experiment 1 (5 males and 1 female, 25 to 33 years old) and 4 subjects in experiment 2 (1 male and 3 females, 22 to 31 years old). Of the 10 subjects, 7 were right-handed and 3 were left-handed. This study was approved by the National Hospital for Neurology and Neurosurgery Ethics Committee.

Stimuli and procedure. Displays with two strings of 3 letters each, centered 2.4° of visual angle above and below fixation, plus 2 flanking grayscale images, centered 2° to the right or left of fixation, cycled on and off every 500 ms (Fig. 1). The images were either places from the MIT campus[6] or young women's faces[4]. The flanking images were always from the same category within a trial, and subtended $3.2 \times 3.7°$. The letter strings each subtended $1.8 \times 1°$. Viewing distance was approximately 30 cm.

Subjects' primary task was to monitor for the occurrence of a target letter X in the letter strings. In addition, they were requested to detect whether a change occurred in one of the two flanking images (defined as the secondary task). Difficulty of letter detection was varied to produce change detection rates of approximately 50%. Scanning was preceded with a practice session in which subjects monitored for X among B, G, N, Q, V and Z. These same non-target letters were used during scanning, or they were replaced with K, M, N, V, W and Z to increase monitoring difficulty, or with B, C, G, O, D and Q to decrease difficulty. The target X appeared in 31% of the displays and subjects were instructed to make a button press as quickly as possible whenever it appeared.

Subjects were requested to respond to the presence or absence of a change at the end of a trial with four displays (that is, three potential changes), and were given two seconds at the end of each trial in which to make their responses. To ensure that the secondary change detection task could be performed without foveation, a change involved replacing an entire image with another image from the same category (for example, one face was replaced with another), rather than changing just a part of the image.

To minimize guessing, subjects were asked to adopt a strict criterion for responding 'change.' This request was successful, with an average false alarm rate of only 1.4% for the change detection task across all 10 subjects. This extremely low false alarm rate suggests that subjects not only had high confidence in their reports, but also based them on full awareness of the change.

Subjects received four runs of 96 trials each, with each run having a different random order of the following trial types (frequency per run in parentheses): face changes (25%), place changes (25%), face no change (12.5%), and place no change (12.5%). In addition, on 25% of the trials, only the fixation cross appeared for the entire 6-s trial. These trials served as a fixation baseline and were randomly intermixed with the stimulus trials. The presence of an X in the primary letter task was also random with respect to the four trial types and was equally likely to occur in each of the four displays within a trial. There were four different images for each of the face/place categories. All possible combinations of the four image identities occurred within a run, with their right/left positions reversed across runs.

Subjects made manual responses to both change and no change trials, using three fingers on their right hand to respond change, no change, or to the presence of an X.

Eye movement monitoring. Long-range infrared video-oculography (ASL 504LRO Eye Tracking System, Massachusetts) was used to continually sample eye position at 60 Hz during functional imaging in experiment 2 (ref. 27). Calibration before scanning was complemented by repeated fixation trials during scanning to compensate for head movements. Data were digitized for analysis. Horizontal eye position was determined for every 100-ms interval in which an image was on the screen, for each trial in every subject. Resulting estimates of horizontal eye

position were determined for each type of trial separately and combined to produce a frequency histogram of eye position (Fig 4).

Functional imaging. A 2T Siemens VISION system was used to acquire blood oxygenation level-dependent (BOLD) contrast image volumes. Each image volume comprised 32 3-mm axial slices with an in-plane resolution of 3 × 3 mm positioned to include both frontal and posterior temporal cortex. Volumes were acquired continuously every 2800 ms (or 3170 ms for subject 1), and trials occurred every 6200 ms. A total of 888 functional volumes were acquired in 4 separate runs for each subject (only 666 functional volumes for subject 3 due to scanner malfunction).

Data analysis. Imaging data were analyzed using standard linear regression techniques implemented in SPM99 (http://www.fil.ion.ucl.ac.uk/spm). The first six scans of each run were discarded to allow for T1 equilibration effects, and the imaging series was then realigned, spatially normalized and smoothed with an isotropic 10-mm Gaussian kernel[28,29]. Voxels that were activated during the experimental conditions were identified using a statistical model containing delayed boxcar waveforms. Each experimental condition in each subject was represented by a boxcar regressor that was positive for the duration of trials of that condition (six seconds) and zero elsewhere. Using a shorter boxcar of four seconds (corresponding to the duration of just the visual events) produced no difference in the location of the activated areas. Each boxcar was then delayed by convolution with a canonical hemodynamic response function, mean-corrected and regressed upon the data with standard linear regression. In addition, high-pass filtering removed subject-specific drifts in signal, and global changes in activity were removed by proportional scaling. Linear contrasts between different regressors representing the different experimental conditions allowed determination of activated areas by creating a spatially distributed map of the t statistic (SPM{t}). The map was thresholded for initial inspection at $p < 0.001$, uncorrected for multiple comparisons. Resultant regions of activation were then jointly characterized in terms of their peak height and spatial extent (cluster size) in order to calculate a p-value, which was then corrected for multiple comparisons across the entire brain volume at a statistical threshold of $p < 0.05$.

For the random effects analysis, a single mean image for each subject was generated by computing subject-specific contrasts between experimental conditions. These images (one per contrast per subject) were then used as the basis for intersubject comparisons, and the resultant regions of activation were characterized and corrected for multiple comparisons in the manner described above.

Acknowledgements

We thank N. Kanwisher for providing the face and place images, and J. Driver for his comments on the manuscript. This work was supported by a Biotechnology and Biological Sciences Research Council grant (N.L.), a Medical Research Council career award (N.L.) and The Wellcome Trust (G.R., C.F.).

Received 30 January; Accepted 10 April 2001

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