

Object-completion Effects in the Human Lateral Occipital Complex

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The ability of the human visual system to recognize partially occluded objects is a striking feat, which has received extensive psychophysical documentation. Here we studied the manifestation of completion effects in the functional magnetic resonance imaging (fMRI) activation of high-order object areas (the lateral occipital complex — LOC). Subjects were presented with three types of images: (i) whole line drawings of animal or unfamiliar shapes ('whole'); (ii) the same shapes, occluded by parallel stripes which occupied roughly half of the surface area of the images ('grid'); and (iii) the same stripes, 'scrambled' so that the relative position of the regions between the stripes was changed while the local feature structure remained intact. Behavioral measurements showed a high degree of object completion in the 'grid' condition, but not in the 'scrambled' condition. The fMRI results show a significantly higher activation to the 'grid' images compared to the 'scrambled' images. This enhanced activation indicates the operation of non-local completion effects, since the local features in both sets of images were the same. The cortical regions showing the highest 'completion' effects co-localized with regions in the LOC which showed the highest activation to the 'whole' images compared to the 'scrambled' images. Activation in early retinotopic areas was similar in both the 'grid' and the 'scrambled' conditions. Our results point to the LOC as a central site in which object completion effects are manifested.

Introduction

A striking characteristic of the human visual recognition process is its ability to overcome obstructions in the retinal image and to 'complete' the missing image elements, so that recognition remains largely unaffected by such obstructions (Snodgrass and Feenan, 1990; Sekuler *et al.*, 1994; Behrmann *et al.*, 1998; Kellman *et al.*, 1998; Rauschenberger and Yantis, 2001). Thus, we can easily recognize a stationary animal in a zoo, despite the fact that its shape is completely segmented by the intervening cage bars. The ability to carry out visual interpolation is critical, as visual scenes are commonly occluded and the visual image fragmented. The phenomenon of picture completion is also an ubiquitous property of various types of neural network models (Williams and Jacobs, 1997; Ullman, 1998). Such networks, upon presentation of a partial input pattern, can settle quite rapidly into an attractor state corresponding to the complete stored pattern.

To what extent are completion effects evident in the activity of specific areas within human visual cortex? Recently, an electrophysiological study using high-density electrical mapping (Doniger *et al.*, 2000) has reported a focus of event-related potential (ERP) activity correlated with visual completion processes. The focus of this activity appears to correspond to a high-order object-related region situated in occipito-temporal cortex, termed the lateral occipital complex (LOC) (Malach *et al.*, 1995). Because ERP measurements are drastically different from blood oxygenation level dependent (BOLD) functional

magnetic resonance imaging (fMRI) in their spatio-temporal profile, we have conducted a functional imaging study in order to map in detail the involvement of the LOC and neighboring areas in the completion of visual images.

Another phenomenon, which is reminiscent of the completion process, is perception of a whole shape in displays containing illusory contours — although not an image completion phenomenon in the strict sense, illusory contours and particularly the Kanizsa triangle, can be viewed as producing an activation wave that spreads beyond the local object features. Again, the object-related LOC was found to be strongly activated by illusory contours (Mendola *et al.*, 1999). Finally, in a previous study, (Lerner *et al.*, 2001) we have found that the LOC was hardly affected when object and face images were cut into halves and exchanged positions. While this effect could indicate that optimal feature size is smaller than half a face, it is also compatible with a completion effect. It may be that in such images the neuronal network completes each half of the face or object into the full-object representation. Thus, converging evidence suggests the LOC as a likely candidate to mediate the operation of completion effects.

In the present work, using fMRI, we mapped the manifestation of completion effects in human visual cortex by comparing the cortical activation produced by intact, partially occluded and 'scrambled' images of familiar and unfamiliar objects. Note that in the latter two conditions, the set of the local image features was matched. Our results reveal the presence of significant completion effects in high-order visual cortex that go beyond the local feature structure of object images.

Materials and Methods

MRI Setup

Subjects were scanned in a 1.5 Signa Horizon LX 8.25 GE scanner equipped with a quadrature surface coil (Nova Medical Inc., Wakefield, MA), which covered the occipital, posterior parietal and posterior temporal lobes. BOLD contrast was obtained with gradient-echo echo-planar imaging (EPI) sequence ($T_R = 3000$, $T_E = 55$, flip angle = 90° , FOV = 24×24 , matrix size 80×80). The scanned volume consisted of 17 nearly axial slices of 4 mm thickness and 1 mm gap. This covered most of the cerebral hemispheres, with the exception of the top part of the parietal lobe (~15 mm). Spin-echo T_1 -weighted high resolution ($1 \times 1 \times 1$ mm) anatomical images (124 slices, 1.2 mm thickness) and 3-D spoiled gradient echo sequence ($T_R/T_E = 40/9$, flip angle = 30° , image matrix 256×256 , 22 min) were acquired on each subject in order to allow exact cortical segmentation, reconstruction and volume statistical analysis of signal changes during the experiment.

Experimental Procedure

Subjects

Eleven healthy subjects (six males, aged 19–50 years, two left-handed) with normal or corrected-to-normal vision took part in one or more experiments (six subjects in experiment 1, five subjects in experiment 2

and five subjects in experiment 3; two subjects took part in all studies). All subjects were given detailed instructions for the experiment and provided written informed consent. The Tel Aviv Sourasky Medical Center approved the experimental protocol.

Stimuli

The stimuli, generated on a PC, were presented with an LCD projector (Epson MP 7200) onto a translucent screen. Subjects viewed them in a mirror positioned ~45° above the forehead.

Experiment 1. The stimuli were presented in a pseudo-random short epoch design – epochs containing visual stimuli were alternated with

epochs of blanks. The visual stimuli were line-drawings of animals (126 pictures, size of 14 × 12°) obtained from various commercial CD databases and converted to line drawings through high-pass and thresholding using Adobe Photoshop 5.0 software package (Adobe Systems Inc.). There were three types of visual epochs in the experiment (see Fig. 1): ‘whole’ epochs that contained the full animal images; ‘grid’ epochs that consisted of the same images but with superimposed grid of green vertical stripes (each stripe 1.2 × 12°, the borders of the stripes were smoothed); and ‘scrambled’ epochs, in which positions of object-stripes were changed relative to their positions in the ‘grid’ epochs – two examples of these are shown by dashed gray arrows (Fig. 1a). Note that the ‘grid’ and ‘scrambled’ epochs consisted of the same group of local features, because

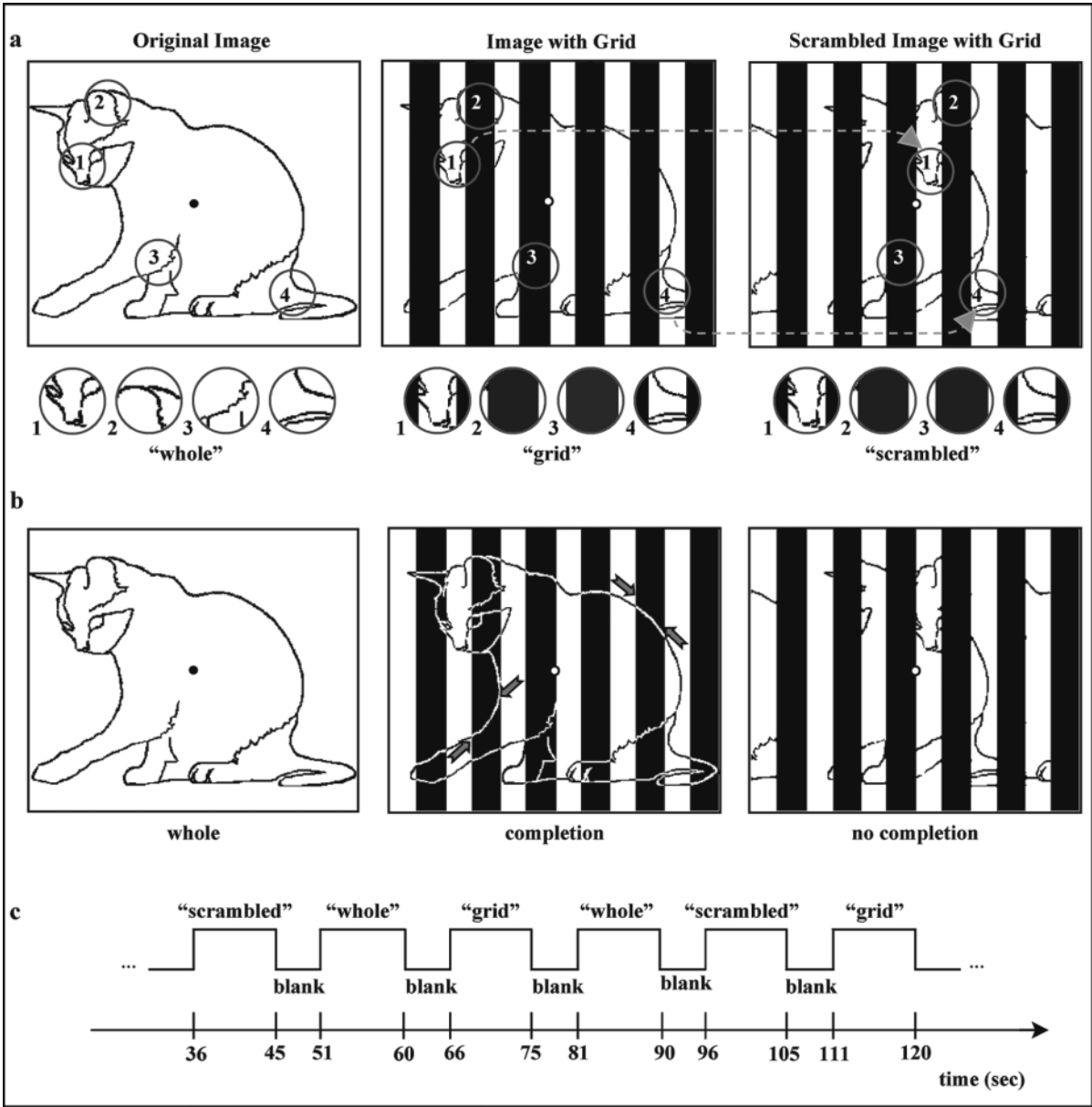


Figure 1. Completion effects for animal shapes (experiment 1): stimuli and experimental paradigm. Examples of the three types of the visual stimuli that were used in experiment 1. An interleaved short epoch design was used (see Materials and Methods). Each epoch consisted of 18 different stimuli (animal line drawings) of the depicted type which included unoccluded (‘whole’) images, same image occluded by an opaque green grid (‘grid’) and the grid with the relative positions of inter-stripes randomly exchanged (‘scrambled’). A red fixation point was presented centrally in all images. (a) Local feature structure illustrated by sampling the images with four local small apertures (circles). Note that the ‘grid’ and ‘scrambled’ conditions have identical sets of local features, while the unoccluded ‘whole’ condition contains a richer set of object elements. Two dashed gray arrows indicate the examples of position changes of object-stripes in ‘scrambled’ epochs relative to their positions in the ‘grid’ epochs. (b) Completion effects. Since the global object configuration was maintained in the ‘grid’ epochs (light gray lines that are denoted by arrows), image completion effects are plausible, while these effects are essentially eliminated in the ‘scrambled’ epochs. (c) A segment from the time axis of the experiment which lasted 339 s. The experiment consisted of 21 visual epochs of 9 s each. Each condition was repeated seven times using different animal images.

the feature arrangement within each individual object stripe remained unchanged. The 'whole' condition consisted of a richer set of local object features since no obstruction was involved in these images. This is illustrated by the four small circles with local object features below the images (Fig. 1*a*); note, though, that the 'whole' condition did not contain the opaque grid. A red fixation point was presented in the center of all pictures. Each epoch consisted of 18 different images presented in 9 s (500 ms per image) with inter-epoch intervals of 6 s blank screen containing a fixation point only. At the beginning and end of the scan there were long blank periods (21 and 9 s, respectively). Epochs of different conditions were interleaved in pseudo-random order. A schematic representation of the temporal sequence of events during an experiment is illustrated in Figure 1*c*. Each scan consisted of 21 epochs – seven epochs for each category. The subjects were requested to covertly name the objects in all epoch types. In the 'scrambled' cases they were asked to guess if they could not recognize the images.

Experiment 2. In a second version of the completion experiment, the original experiment was modified in two ways. (i) All subjects performed a one-back memory task, in which they were asked to determine whether two consecutive images were identical or not. (ii) The same images were used as in the first completion experiment, but this time pictures were presented for 250 ms interspersed with 250 ms blanks. Again, each visual epoch contained 18 different images and continued for 9 s; inter-epoch blanks lasted 6 s. The first and the last blanks were 21 and 9 s, respectively.

Experiment 3. The third experiment had exactly the same experimental conditions and short-epoch design as experiment 1, but in this case unfamiliar novel objects (fractal patterns, Fourier descriptors and self-made images, 126 pictures, size 14 × 12°) were used (Fig. 10). The subjects were asked to fixate on a central red point and passively view the images.

Mapping Borders of Visual Areas

The representation of vertical and horizontal visual field meridians was mapped in the same subjects to establish the location of retinotopic areas based on anatomical and functional characteristics (DeYoe *et al.*, 1996; Tootell *et al.*, 1996). Details of the procedure are as previously published (Grill-Spector *et al.*, 1998). Briefly, visual stimuli consisted of triangular wedges that were presented either vertically (upper or lower) or horizontally (left or right) meridians. The wedges included either gray-level natural images or black and white objects-from-texture pictures. The visual stimuli were presented at a rate of 4 Hz in 18 s blocks alternated with 6 s blanks. Subjects were required to fixate on a small cross in the center of images.

Measuring Naming Performance

For each subject, naming performance was measured outside the magnet ~4 weeks after the fMRI scan. Subjects were asked to overtly name the animal images as specifically as possible. Performance was measured as percentage of correct naming. The order of stimuli was the same as that in the fMRI scan, except that each stimulus was presented for 500 ms, followed by a 1500 ms blank to allow sufficient time for overt naming of each image.

Data Analysis

All fMRI data were processed using the 'BrainVoyager 4.2' software package (Goebel *et al.*, 1998a,b) and in-house software. The cortical surface was reconstructed from the subject's structural MRI. Surface reconstruction included the segmentation of the white matter by grow-region function, the smooth covering of a sphere around the segmented section and the expansion of the reconstructed white matter into the gray matter. Following surface reconstruction, the brain was 'inflated' so as to allow sulcal as well as gyral cortex to be viewed. The surface was cut along the calcarine sulcus and unfolded into the flattened format.

Data analysis was done separately for each subject in each scan. The preprocessing procedure consisted of head motion correction and high-frequency temporal filtering. The first three images of each functional scan were rejected and a lag of 3 s was used to take account of the hemodynamic response delay. The fMRI activation (2-D images) were

overlaid on corresponding 2-D anatomical slices, incorporated into the 3-D data sets through trilinear interpolation and transformed into Talairach space (Talairach and Tournoux, 1988). Finally, this fMRI activation was placed on the subjects' unfolded cortical surfaces.

Statistical analysis was based on the general linear model (Friston *et al.*, 1995). The signal time-course was correlated for each voxel with a reference function. The reference function for each experimental condition (predictor) was a delayed (3 s) square wave corresponding to the stimulus condition (i.e. 'whole', 'grid' and 'scrambled'). An average time-course was achieved from all voxels within a-priori defined regions of interest (ROI). Three-dimensional statistical maps were obtained according to the degree of correlation to the reference function. Only voxels whose correlation value was > 0.2 ($P < 10^{-5}$, uncorrected) were included in the statistical calculations.

Multi-subject Analysis

In addition to subject-by-subject analysis, we also analysed the data in a multi-subject approach. To obtain the multi-subject maps, the time-courses of subjects were converted into Talairach space, *z*-normalized and concatenated. The statistical tests were performed on the concatenated time-course.

'Internal Localizer' Test

To obtain highly accurate measures of the activation level within the regions of interest, we took advantage of the short-block presentation and adopted a procedure which we termed the 'internal localizer' approach. In this procedure a subset of the epochs served to localize regions of interest, while another subset, not used in the statistical localization tests, was used to evaluate the activation level. Note that this approach has the advantage that the localizer test is done on epochs which were in the same scan in which the activation level was measured (rather than the more common separate localizer scan), thus minimizing inaccuracies due to head motion between scans. However, the measured activity in the other epochs is unbiased, since these epochs were not included in the statistical localizer test. Specifically, for each localizer test (e.g. 'whole' versus 'scrambled') two statistical tests were conducted. In the first test, five of the epochs were used as anatomical localizers, while second and fourth epochs of the same conditions (i.e. 'whole' and 'scrambled') were not included in the test, and the level of activation during these epochs was measured separately. In the second test, the same localizer test was conducted, but this time the second and fourth epochs were included in the localizer test, while the third and fifth epochs of the same conditions were excluded from the test, and their activity level was measured separately.

The average activation from epochs which were used for anatomical localization are presented in the figures as 'Localizer'. The data obtained from all epochs, which were not included in the localizer test (but consisted of the same type of stimuli), were averaged within each subject. These data were averaged across subjects and were presented separately in the histograms.

Results

Manifestation of Completion Effects in the Human Visual Cortex

In order to uncover the neural mechanisms mediating visual completion, we conducted the object-completion experiment 1 shown in Figure 1 (see Materials and Methods for more details). The experiment consisted of three types of images: 'whole', 'grid' and 'scrambled'. Note that the set of local features is identical (up to a change in absolute position) in the 'grid' and 'scrambled' conditions, while the 'whole' condition contains a richer set of local object features. This is illustrated in Figure 1*a* by the four local object features sampled by the small aperture. Note also that the global relationship between adjacent stripes is maintained in the 'grid' condition, but is completely disrupted in the 'scrambled' condition. Figure 1*b* illustrates the fact that, because the global configuration of local elements is maintained

in the 'grid' condition, image completion effects are plausible, while these effects are essentially abolished in the 'scrambled' condition.

In considering the various possible outcomes of this experiment, one can envision two extreme situations (with numerous additional variations and gradations of these possibilities). One possibility is that object areas are completely dominated by very local, independent, object-feature representations. In such a representation we would expect a higher activation to the 'whole' image compared to the occluded cases, since presumably the occlusion removes a substantial fraction of local object features. However, no difference in activation is expected in this case between the 'grid' and 'scrambled' conditions, since an identical set of local features is present in the two conditions. The other extreme case is a network that manifests full completion effects – here we would expect that activation to the 'whole' and the 'grid' images should be identical, since the neuronal representation is capable of completely 'filling in' the occluded object-parts through figure completion effects. On the other hand, the 'scrambled' images should produce much less activation, since they presumably do not lead to figure completion effects.

Before reporting the fMRI data, we present the behavioral findings to document the fact that the paradigm did indeed elicit perceptual completion. Figure 2 shows the naming performance of the nine subjects (six subjects that were scanned in the experiments 1 and 2 and three new subjects) measured outside the magnet for the same images presented during the fMRI scan, but with an average delay of 4 weeks (and no less than 3 weeks) after the scan.

As can be seen, correct naming of the images occluded by the grid was quite high and showed only a small (albeit statistically significant, $P < 0.005$) reduction compared to the recognition of the 'whole' images. In contrast, recognition of the 'scrambled' images was drastically reduced, indicating that the local features were not sufficient to allow an effective recognition level. Thus, perceptual completion effects allowed the subjects to achieve

high naming performance, despite the 50% occlusion of the image's surface area.

Mapping Object-related Areas in the Human Cortex

In order to reveal the cortical activation associated with completion, we first had to functionally define object-related areas. To that end we compared, in visually responsive regions, the relative activation to 'whole' line drawings versus 'scrambled' images. Figures 3 and 4 show the results of such tests on single- and multi-subject maps, respectively. As can be seen, there was a clear transition in the relative activation by the 'whole' compared to the 'scrambled' images, so that as one moves from retinotopic to more anterior visual areas, there was increasingly dominant activation by the 'whole' object images. The regions most dominated by 'whole' images (colored in green/blue) were located in the most anterior-lateral aspects of the visually activated regions and corresponded to the LOC (Malach *et al.*, 1995; Lerner *et al.*, 2001). Table 1 presents the foci of this activation in Talairach coordinates (Talairach and Tournoux, 1988). In contrast, early retinotopic areas showed a slightly higher activation to the 'scrambled' images (orange colors), most likely due to the high spatial frequencies introduced by the occluding bars.

To identify the relative activation in these regions for the three types of stimuli, we sampled from four regions that showed consistent activation to the images presented. The LOC was defined functionally by its preferential 'whole' versus 'scrambled' activation (statistical test 'whole' > 'scrambled'); note, however, that the activation during the 'whole' and 'scrambled' epochs was measured independently from epochs not included in the localizer test (see the 'internal localizer' approach in the Materials and Methods section). The LOC was divided into two putative subdivisions by anatomical criteria as follows (Grill-Spector *et al.*, 1999; Lerner *et al.*, 2001): (i) LO (Grill-Spector *et al.*, 1999) – the lateral occipital region at the posterior part of the inferior-temporal sulcus, usually this focus was located posterior and ventral to area MT; (ii) pFs – posterior fusiform

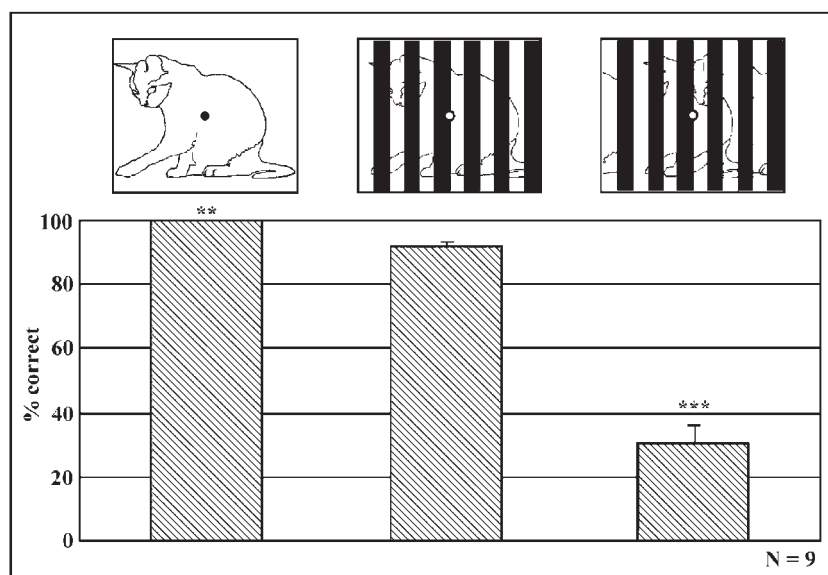


Figure 2. Naming performance during the different conditions. Average naming performance ($n = 9$) is presented for each stimulus type. Images were identical to those used in experiment 1. The icons above the histograms illustrate the type of visual images presented to the subjects during each epoch. The y-axis shows the average percentage of correct recognition. Error bars indicate \pm standard error of the mean (SEM). Asterisks denote significance level calculated by a t -test comparing to 'grid' condition (** $P < 0.005$; *** $P < 0.0005$).

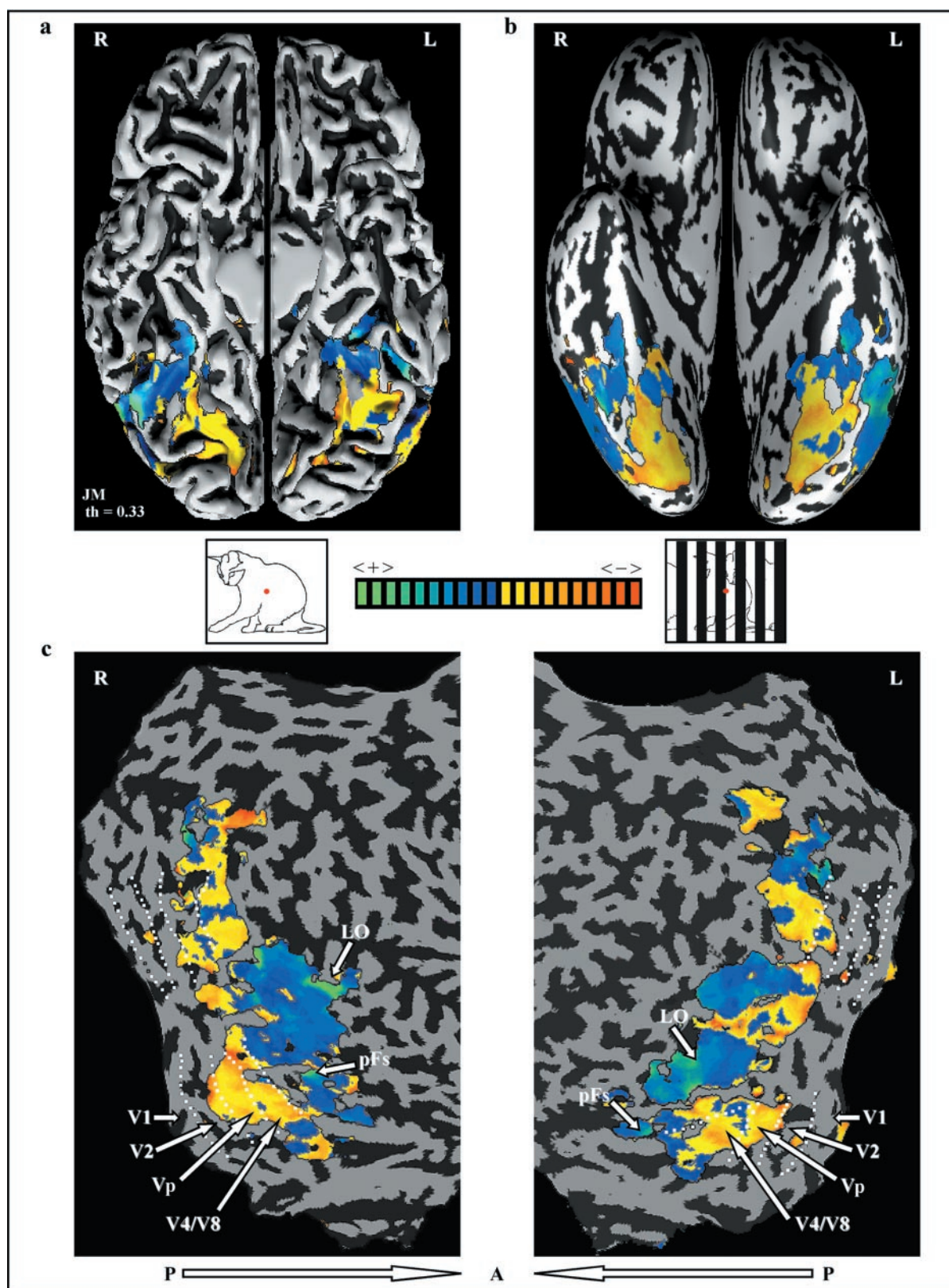


Figure 3. Preferential object activation — single subject maps. Functional activation maps showing relative activation to 'whole' versus 'scrambled' object images from experiment 1 (see Fig. 1) superimposed on the left and right hemispheres of the folded (a), inflated (b) and unfolded (c) cortical surfaces of a single subject. The maps were constructed using GLM (general linear model) statistical analyses, with preferential activation to 'whole' epochs shown in green, compared to 'scrambled' shown in orange. Blue and yellow colors indicate more balanced activation levels. Sulcal cortex is coded darker than gyral cortex. Retinotopic visual areas were defined by superimposing the meridian maps that were obtained on a separate scan. The meridian borders are indicated on the flattened map by white dotted lines and denote the retinotopic areas V1, V2, Vp, V4/V8 (shown by arrows) in the ventral visual pathway. The high-order object-related areas are labeled as LO (lateral occipital) at the posterior part of the inferior-temporal sulcus, and pFs — a focus in the posterior fusiform gyrus. Threshold number (th) indicates the linear correlation coefficients of the fMRI signal with the GLM predictors. A, anterior; P, posterior.

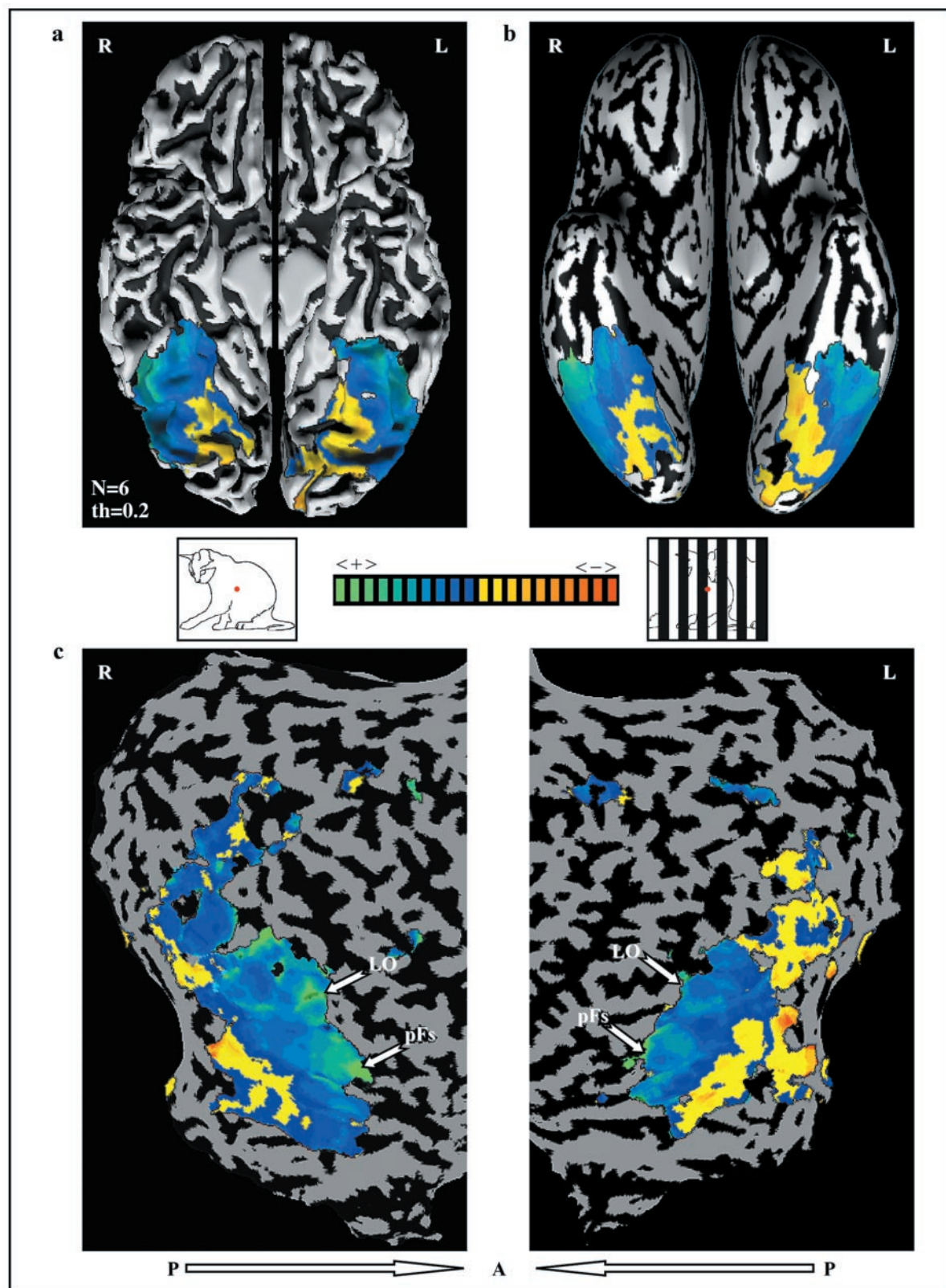


Figure 4. Preferential object activation — multi-subject maps. Averaged functional activation maps (for six subjects) showing the relative activation to 'whole' versus 'scrambled' object images from experiment 1 superimposed on a folded (a), inflated (b) and unfolded (c) cortical surfaces. Same presentation format and statistical test as Figure 3. The arrows label the highest activation to 'whole' images (green). Note the gradual transition to dominance by 'whole' image as one moves anteriorly within the LOC. Anterior–posterior direction is denoted by A and P.

Table 1

The main centers of activation in Talairach coordinates

Location	Completion experiment 1			Completion experiment 3		
	x	y	z	x	y	z
Right hemisphere						
LO	44.8 ± 2.5	-63.5 ± 4.6	-1.5 ± 5.3	46.8 ± 6.9	-55.4 ± 5.3	-0.6 ± 3.8
pFs	35.7 ± 4.8	-48.5 ± 7.9	-14.3 ± 5.1	38.8 ± 7.0	-47.6 ± 10.5	-13.2 ± 3.5
Left hemisphere						
LO	-46.4 ± 3.4	-66.5 ± 8.7	-1.4 ± 7.1	-46.6 ± 4.6	-61.0 ± 7.1	-0.6 ± 4.6
pFs	-40.8 ± 1.6	-52.2 ± 3.2	-14.3 ± 2.4	-42.8 ± 2.2	-49.4 ± 6.7	-12.4 ± 6.0

Talairach coordinates (Talairach and Tournoux, 1988) in the subjects who participated in the first and third completion experiments, respectively (statistical test 'whole' versus 'scrambled'). The coordinates were derived for LOC and pFs foci that were separated based on anatomical criteria: the LOC was located in the lateral aspect of the occipital lobe, while the pFs was situated within the vicinity of the fusiform gyrus. Values represent the mean ± SD in millimeters.

gyrus that is situated lateral and anterior to area V4/V8 with a small gap between them (see Fig. 3). For comparison, we measured activation in the same test in two retinotopic regions (V4/V8 and Vp) which were defined using meridian mapping. V4/V8 is a relatively large retinotopic complex, partially overlapping the second upper vertical meridian representation and the horizontal meridian anterior to it (Hadjikhani *et al.*, 1998). Area Vp is located between V4/V8 and V2, overlapping the second horizontal meridian representation anterior to it.

The results obtained from each of these regions are shown in Figure 5. As can be seen, and in agreement with our previous studies, in the LOC, both in the LO and pFs subdivisions, the activation was significantly higher to the 'whole' images compared to the 'scrambled' images. Importantly, the activation to the 'grid' images was significantly higher compared to the 'scrambled' images ($P < 0.05$ in LO and $P < 0.005$ in pFs). Considering that in terms of the local feature structure the 'grid' and 'scrambled' images were identical, this increased activation can be attributed to the operation of non-local completion effects that transcend the grid lines. On the other hand, the activation to 'whole' images was significantly higher compared to the 'grid' images ($P < 0.05$). This indicates that the completion processes were not sufficient to fully compensate for the occlusion of image parts. In earlier retinotopic areas V4/V8 and Vp, the trend observed in LOC was reversed. Here the activation to both the 'grid' and 'scrambled' images was significantly higher compared to the 'whole' images ($P < 0.05$ for the 'grid' condition in both areas and 'scrambled' condition in area Vp; $P < 0.005$ for the 'scrambled' condition in V4/V8). This trend may reflect a higher activation due to discontinuities and corners introduced into the image by the grid occluder.

Are Completion Processes Performed in a Separate Cortical Area?

It could be argued that object-related regions, defined by their preferential activation to 'whole' compared to 'scrambled' images, are not the optimal sites to search for the operation of completion effects – it could be that object completion requires additional processing operations which are allocated in other cortical areas. To examine this possibility we mapped cortical regions that showed the highest preferential activation to the 'grid' stimuli compared to the 'scrambled' stimuli (statistical test 'grid' > 'scrambled', 'whole' images ignored).

Figure 6 shows the activation pattern revealed by preferential activation to 'grid' images compared to 'scrambled' images. The voxels that were preferentially activated by the 'grid' stimuli were located in the LOC, anterior to retinotopic areas designated by white dotted lines. To examine the relationship of these voxels to object-related regions we superimposed the borders of

clusters preferentially activated by 'whole' images ('whole' versus 'scramble' test), indicated by the purple contour, on these maps. It is clear that the two activity maps overlap substantially. Note also that early retinotopic areas were not activated by either test. Thus, it can be concluded that the same cortical regions, which show the highest object-related activation, also show the highest completion effects.

The activity level observed in the regions preferentially activated by the grid is shown in Figure 7 for the different conditions. As can be seen, the profile of activation was quite similar to that found for the 'whole' versus 'scrambled' test, further demonstrating that the two tests highlighted essentially the same set of voxels.

Completion Experiment 2

To what extent are the results of the completion experiment sensitive to the specific paradigm design? To explore this issue we repeated the completion experiment, but modified two important aspects: image exposure duration and the subject's task. Thus, we changed the task to a one-back memory task in which the subject had to identify whether two consecutive images were identical or not. It should be noted that performing this task on the 'scrambled' images was much more difficult and undoubtedly involved a higher attentional demand. Second, images were presented for 250 ms, followed by 250 ms fixation – such duration is sufficient for completion effects (Rauschenberger and Yantis, 2001), but precludes lengthy contemplation and scanning of the image.

The results of this modified experiment performed on five subjects are shown in Figure 8. Voxels were chosen using the 'internal localizer' approach (see Materials and Methods). The results are quite similar to the results obtained in experiment 1 (see Fig. 5). In particular, there was a small but not statistically significant difference in the activation during the 'grid' condition between the two experiments (LO, $0.95 \pm 0.1\%$ in the first experiment and $0.91 \pm 0.2\%$ in the second; pFs, $1.04 \pm 0.1\%$ in the first experiment and $0.95 \pm 0.2\%$ in the second). This effect may be due to the shorter presentation duration (see Discussion).

Testing for Priming Effects

It has been reported that previous exposure may change both the behavior and fMRI signal in high-order object areas (Biederman and Cooper, 1991; James *et al.*, 2000). In the present experiments, the design was not intended to examine such effects since we used a large number of different images. However, to examine the potential impact of such exposure in the experiment, we analysed separately the activation in 'grid' epochs in which subjects saw the image for the first time (three

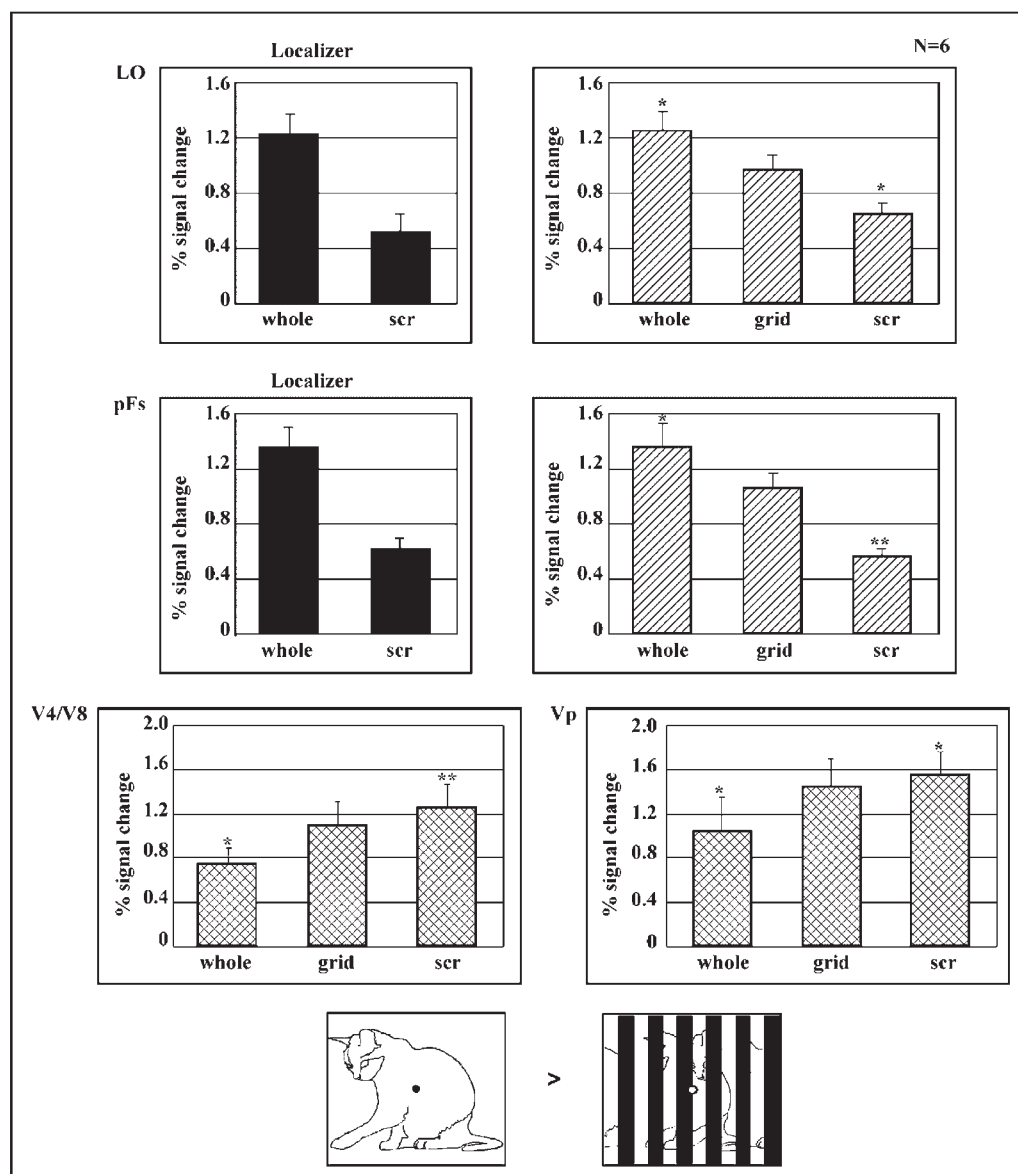


Figure 5. Object completion as reflected in the activation profiles in experiment 1. Activation profiles obtained from the LOC (a) and retinotopic visual areas V4/V8 and Vp (b) for the different conditions of experiment 1. Criteria for regions of interest and, in particular, the 'internal localizer' approach, are described in detail in the Materials and Methods. The y-axis denotes fMRI activation level (percentage signal change) relative to blank epochs. Asterisks denote a significant difference compared to the 'grid' condition calculated by a *t*-test (* $P < 0.05$; ** $P < 0.005$). Note the enhanced activation in the 'grid' condition compared to the 'scrambled' condition, which can be attributed to completion effects. Error bars show \pm SEM calculated across subjects.

epochs), with those epochs which followed prior exposure to the 'whole' image (three epochs). The results of this analysis are shown for LO and pFs in Figure 9a and for the recognition performance in Figure 9b. In both regions there appeared to be a significant trend for a slightly higher activation after exposure to the 'whole' stimulus compared to prior to exposure (in LO $P = 0.007$; in pFs $P = 0.048$). A similar but not statistically significant ($P = 0.2$) trend could be observed in the recognition performance (Fig. 9b).

Completion Effects for Unfamiliar Objects

To explore whether the completion effects we have observed so far were unique to familiar objects, we ran a third experiment in which unfamiliar objects were used instead. The design of the experiment is shown in Figure 10. It was identical to experi-

ment 1 (Fig. 1), with the exception that unfamiliar fractal and Fourier descriptors served as the objects.

As in experiments 1 and 2, we defined the regions of interest in the LOC by the contrast 'whole' > 'scrambled'. Based on anatomical criteria (see Materials and Methods) we divided the region of activation into LO and pFs foci. The level of completion effects was estimated, as in experiments 1 and 2. Again, the activation during the 'whole' and 'scrambled' epochs was obtained independently from visual epochs not included in the localizer test (see Materials and Methods). The results of this analysis are shown in Figure 11. In both LO and pFs, the activation was significantly higher to the 'whole' images compared to the 'scrambled' images. Moreover, the activation to the 'grid' images was significantly higher compared to the 'scrambled' images ($P < 0.05$ in LO and $P < 0.005$ in pFs). Thus, we can conclude that

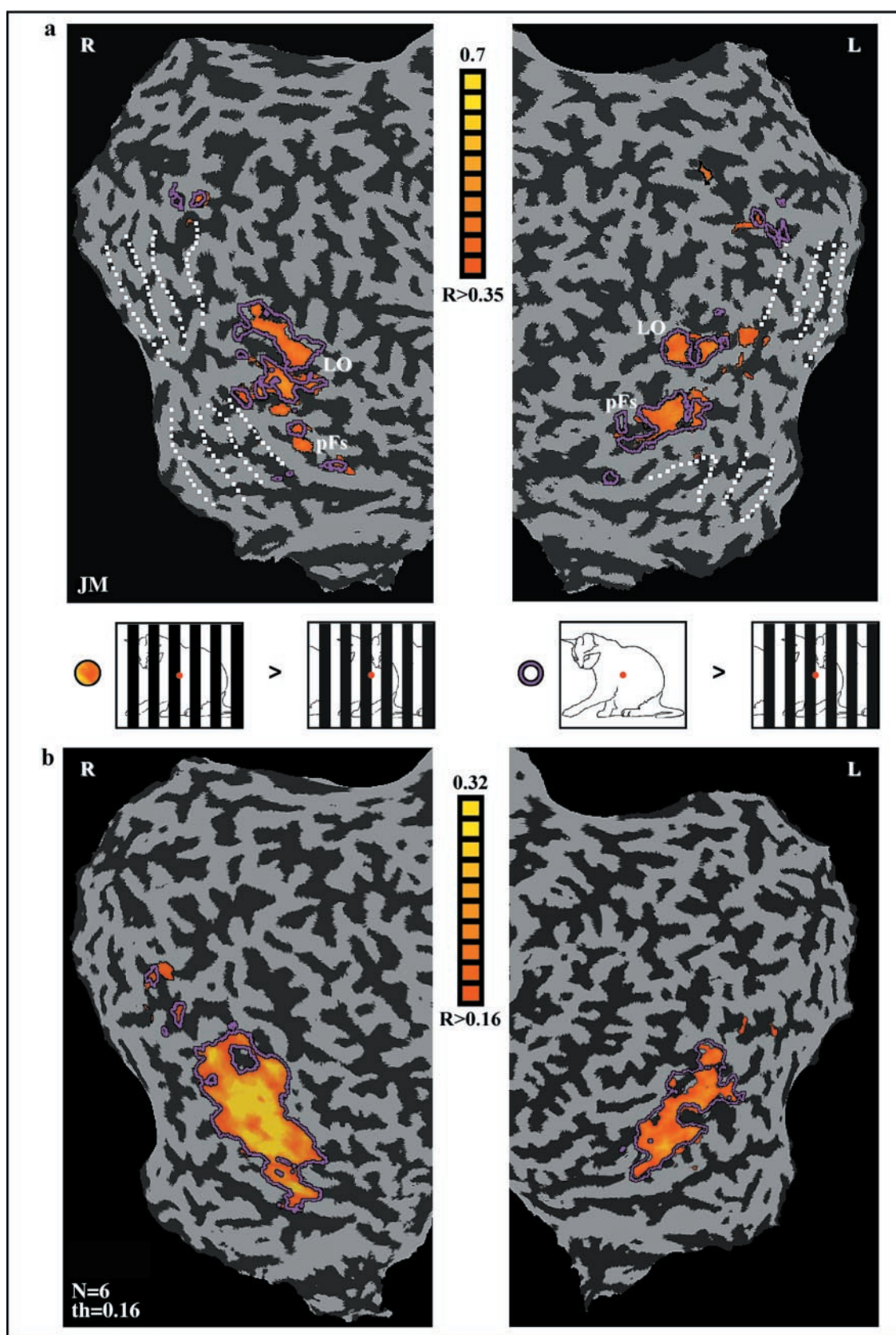


Figure 6. Co-localization of preferential 'whole' and 'grid' activation. Superposition of activation maps on unfolded cortical surfaces of two hemispheres from one subject (a) and average functional activation maps from six subjects (b) in experiment 1. The maps show the location of regions with preferential activation in the 'grid' versus 'scrambled' paradigm (statistical test 'grid' > 'scrambled'). To compare the location of these regions to the 'whole' versus 'scrambled' maps, the borders of preferentially active voxels in the latter test were delineated in purple and superimposed on the statistical map. Note the substantial overlap between these two maps. The activated voxels were located in two major foci: LO and pFs. Meridian borders are indicated in the same manner as in Figure 3. The color scale indicates the linear correlation coefficients of the fMRI signal with the GLM predictors.

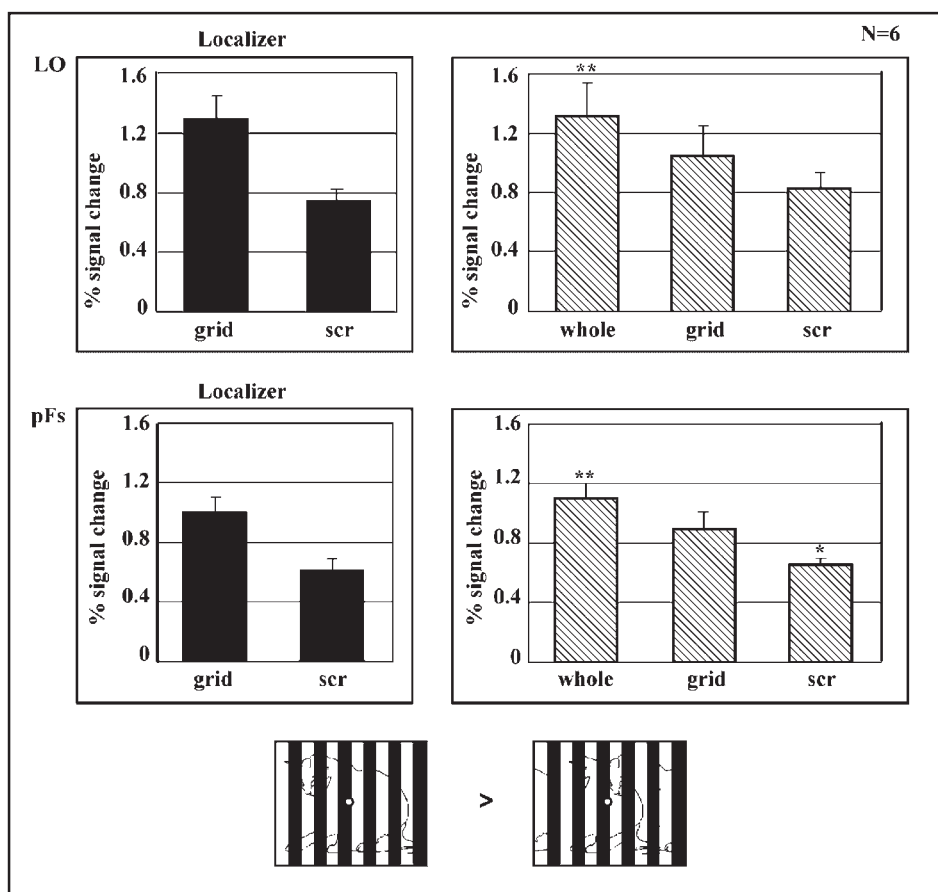


Figure 7. Activation profiles in the 'grid' versus 'scrambled' test in experiment 1. Histograms show the average activation ($n = 6$) derived from the LO and pFs regions in the 'grid' versus 'scrambled' test of experiment 1. ROI selection criteria were the same as in Figure 5, except that here the statistical test was 'grid' > 'scrambled'. The y-axis shows percentage signal change calculated relative to blank epochs. Asterisks present a significant difference compared to the 'grid' condition calculated by a t -test (* $P < 0.05$; ** $P < 0.005$). Error bars indicate \pm SEM computed across subjects.

the completion effects observed in experiments 1 and 2, using familiar animal figures, can be extended to unfamiliar shapes.

In general, the activation to the unfamiliar images was somewhat noisier compared to the animal figures. However, despite some variability, the loci of LO and pFs activation were consistent with in experiments 1 and 3 (see Talairach coordinates, Table 1).

Discussion

Completion Effects in Human High-order Object-related Areas

The use of rectangular stripes as occluders allowed us to compare the activation to occluded and 'scrambled' images which contained an identical set of local features – since the local object elements in each inter-stripe region were identical in both images (see Fig. 1*a,b*). Note that our definition of 'local' pertains to sizes not larger than the width of an inter-stripe region. Our finding of a significantly higher activation in the occluded case compared to the 'scrambled' case indicates that completion processes that go beyond the local feature structure contribute to the object-selective activation in high order object areas, i.e. LOC. Our study could not provide an exact measure of the spatial range of the completion effects involved. It is possible that the completion involved the entire object template or, alternatively,

large object 'chunks' that span more than a single stripe and were consequently disrupted in the scrambling operation.

Regardless of their range, the completion effects found here provide further demonstration of the operation of long-range holistic processes in high-order human object areas. Such effects were reported in the case of illusory contours (Hirsch *et al.*, 1995; Mendola *et al.*, 1999; Hasson *et al.*, 2001) and in perception of object volume (Moore and Engel, 2001). The results also illustrate the similarity between naming performance, which also shows a strong completion effect (Fig. 2) and fMRI activation.

On the other hand, the activation to the occluded figure did not reach the level of activation produced by the whole, unoccluded images. We can envision a number of possible reasons for this lower activation level. First, it could be that for some images the occlusion was too extensive and prevented the operation of full completion effects. This possibility is actually reflected in the behavioral results, which show a slightly lower recognition level for the occluded as compared to the 'whole' images (Fig. 2).

Alternatively, it could be that the representation of objects in the LOC contains a mixture of neurons, some sensitive to local features while others are activated by more holistic aspects of the images. Such a mixture can not be differentiated at the resolution of fMRI. One way to by-pass such resolution limit is through object adaptation effects (Grill-Spector *et al.*, 1999).

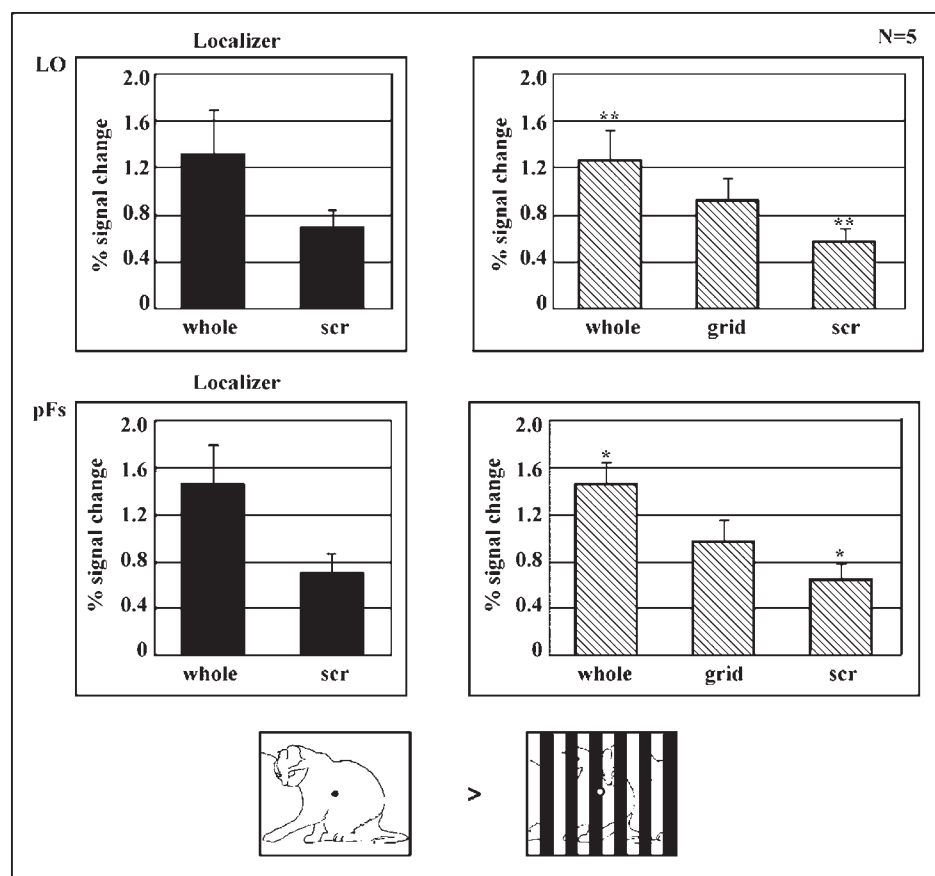


Figure 8. Completion effects for animal shapes (experiment 2) — activation profiles in the LOC. Histograms demonstrate the activation profiles for LO and pFs obtained from the five subjects in the 'whole' versus 'scrambled' test in experiment 2, in which a one-back memory test was used (see Materials and Methods). Epochs used in the statistical test are shown as Localizer (see Materials and Methods). The x-axis symbolizes the type of stimuli and the y-axis represents fMRI activation level relative to blank epochs (percentage signal change). Asterisks indicate a significant difference compared to the 'grid' condition computed by a t-test (* $P < 0.05$; ** $P < 0.005$). Error bars specify SEM estimated across subjects.

Interestingly, a recent report has demonstrated, using adaptation effects, that LOC neurons can be sensitive to the global configurational aspects of objects rather than their local feature structure (Kourtzi and Kanwisher, 2000a). This result supports the notion that at least some of the neuronal populations in the LOC show full completion effects.

Finally, an interesting possibility is that the partial completion actually reflects a rapidly evolving transformation of the object representation from one dominated by local features to a more holistic representation manifesting completion effects (Sekuler *et al.*, 1994; Rauschenberger and Yantis, 2001). Intriguing single unit evidence for such behavior was provided recently by R. Born and his colleagues in macaque MT, where the neuronal population underwent, in the span of ~100 ms, a transformation from component to holistic response to moving plaids (Pack *et al.*, 2000). One way to explore this possibility is through rapid masking paradigms (Grill-Spector *et al.*, 2000), which may allow the temporal separation of early and late events in object representation. The slight reduction in 'grid' activation when presentation time was shortened (Fig. 8) in the second experiment is compatible with this notion. However, this question will need a detailed parametric study to be clarified.

A Separate Area for Object Completion?

It could be argued that, since the process of picture completion is so fundamental to human vision, it may have engaged specialized mechanisms located separately from the more automatic

aspects of whole-object representation. We searched specifically for such regions, but found that they largely coincided with the regions that were preferentially activated to the 'whole' images (Fig. 6). Thus, we can conclude that the cortical mechanisms involved in completion effects co-localize with regions activated by the unoccluded object image.

This finding relates to the more general question of the manifestation of recognition difficulty in fMRI activation. It may appear intuitively that more difficult recognition processes necessitate more computational resources, engage more intense attentional effects and consequently should involve enhanced cortical activation. As our completion results show, the inverse is true; pictures that are more difficult to recognize produce a weaker activation level. This result is in agreement with previous studies that showed that image degradation which makes recognition more difficult reduces rather than enhances fMRI activation (Malach *et al.*, 1995; Haxby *et al.*, 2000).

More recently, in a paradigm quite similar to the completion experiment reported here, it was found that fMRI activation in high-order object areas is enhanced as the level of object occlusion is reduced (Goodale, 1998). In fact, the only instance in which enhanced recognition performance was associated with reduced fMRI activation was in priming effects and even here it is not clear whether this reduction is not confounded by concurrent adaptation effects (Goodale, 1998; Grill-Spector and Malach, 2001). Thus, it appears that the level of fMRI activation is correlated to the recognition performance rather than to

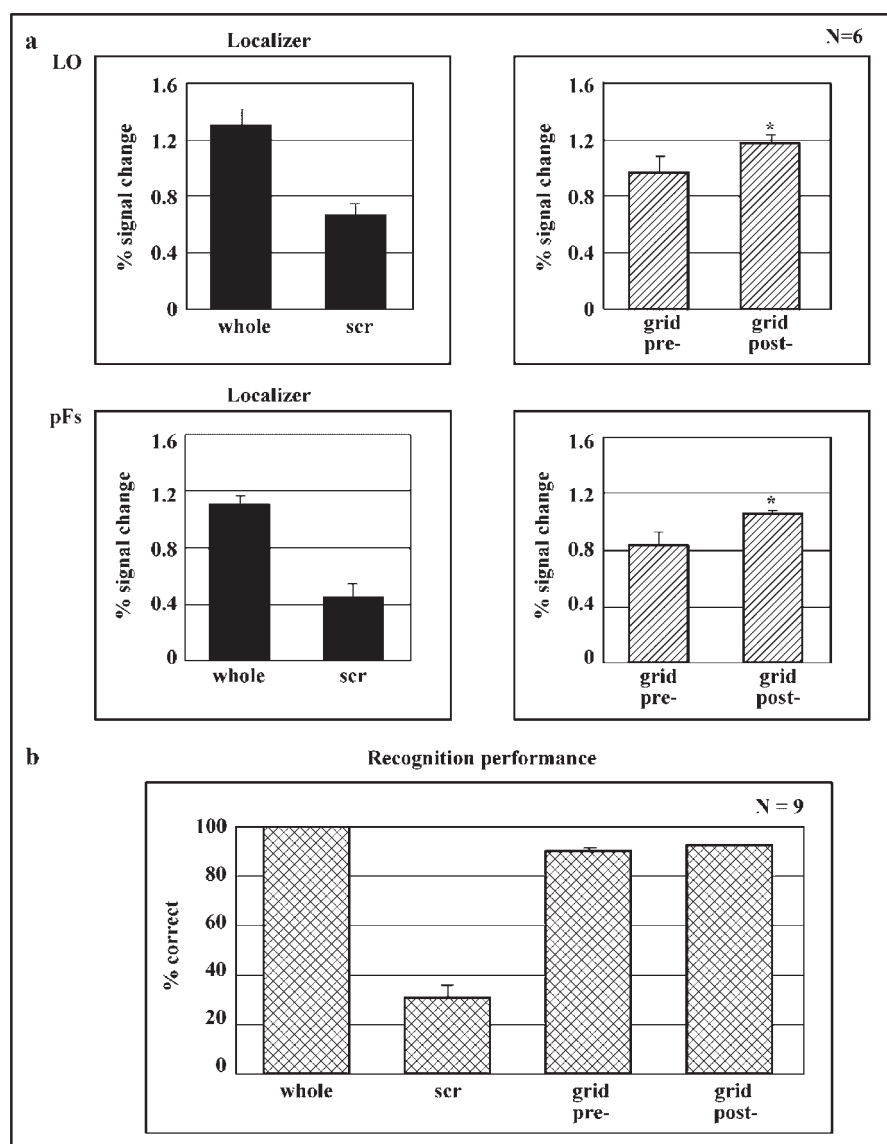


Figure 9. Searching for priming effects in activation and naming performance. (a) The results of a separate analysis for the activation in ‘grid’ epochs, in which subjects saw the image for the first time (first three epochs) and epochs which followed prior exposure to the ‘whole’ image (last three epochs) are shown for LO and pFs. The y-axis shows percentage signal change calculated relative to blank epochs. Error bars indicate SEM across subjects. Note that, after exposure to the ‘whole’ stimulus, activation is slightly higher compared to prior to visual experience (in LO $P = 0.007$; in pFs $P = 0.048$). Asterisk indicates the statistical significance calculated by t -test. (b) Same analysis for the correct naming performance averaged across nine subjects. A slight enhanced performance could be observed following exposure to the whole image (not statistically significant, $P = 0.2$). The x-axis indicates category of stimuli and the y-axis shows the averaged correct recognition (%).

recognition ‘effort’ – this should put important constraints on the type of models relevant to human recognition.

Hierarchical Organization within the Lateral Occipital Complex

In a previous report (Lerner *et al.*, 2001) using a gradual object scrambling paradigm, we have found evidence for a putative posterior-to-anterior hierarchical axis extending from retinotopic areas into the LOC itself, so that sensitivity to image scrambling was gradually increased at higher levels of the putative hierarchy. Here, using the ‘whole’ versus ‘scrambled’ test, we found a further suggestion for such organization. This was particularly evident when combining the activation maps across subjects (Fig. 4). The putative hierarchy was clearer in the right hemisphere and was manifested in the gradual transition from blue to green colors, indicating increased selectivity to

‘whole’ object representation as one moves anteriorly. In the present results this hierarchical trend appeared to split into two anatomical branches (Fig. 4, arrows) – a dorsal branch corresponding to the LO region and a ventral branch corresponding to the pFs. However, the possibility can not be ruled out that the anterior foci may form a continuous band, had additional object categories been used.

Sensitivity to Experimental Conditions

Comparing the results of completion experiments 1 and 2 showed that the main completion effect was not dependent on a lengthy contemplation of the images, since using short (250 ms) image presentation times did not affect the results substantially. Similarly, task-related effects such as attentional load and recognition strategy were changed substantially in the one-back memory task compared to the naming task used in experiment 1

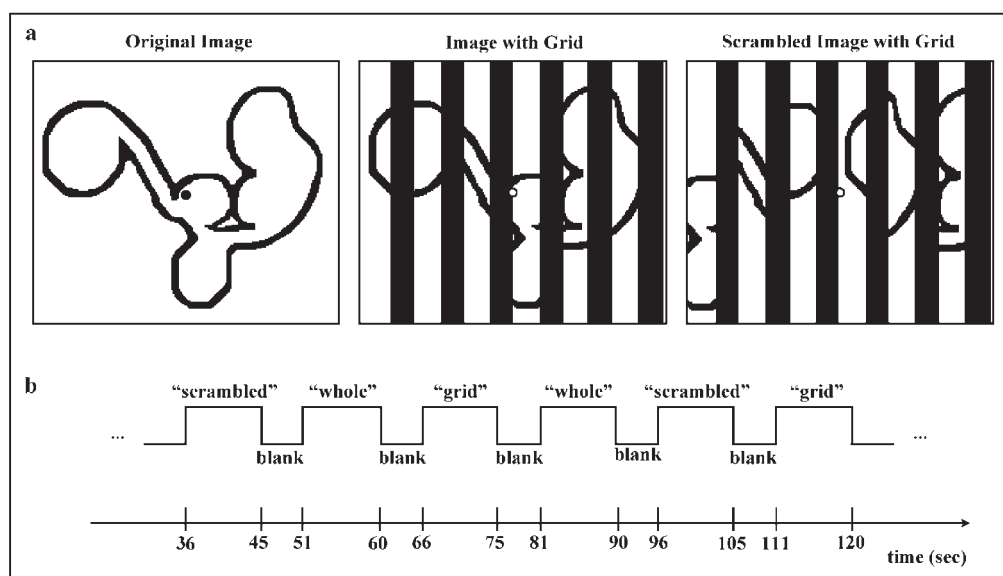


Figure 10. Completion effects for novel objects (experiment 3): stimuli and experimental paradigm. Examples of the visual stimuli that were used in experiment 3. An interleaved short epoch design was used (see Materials and Methods). Each epoch consisted of 18 different stimuli (animal line drawings) of the type depicted, which included unoccluded images ('whole'), same image occluded by a green grid ('grid') and the grid but with the relative positions of inter-stripes randomly exchanged ('scrambled'). A red fixation point was presented centrally in all images.

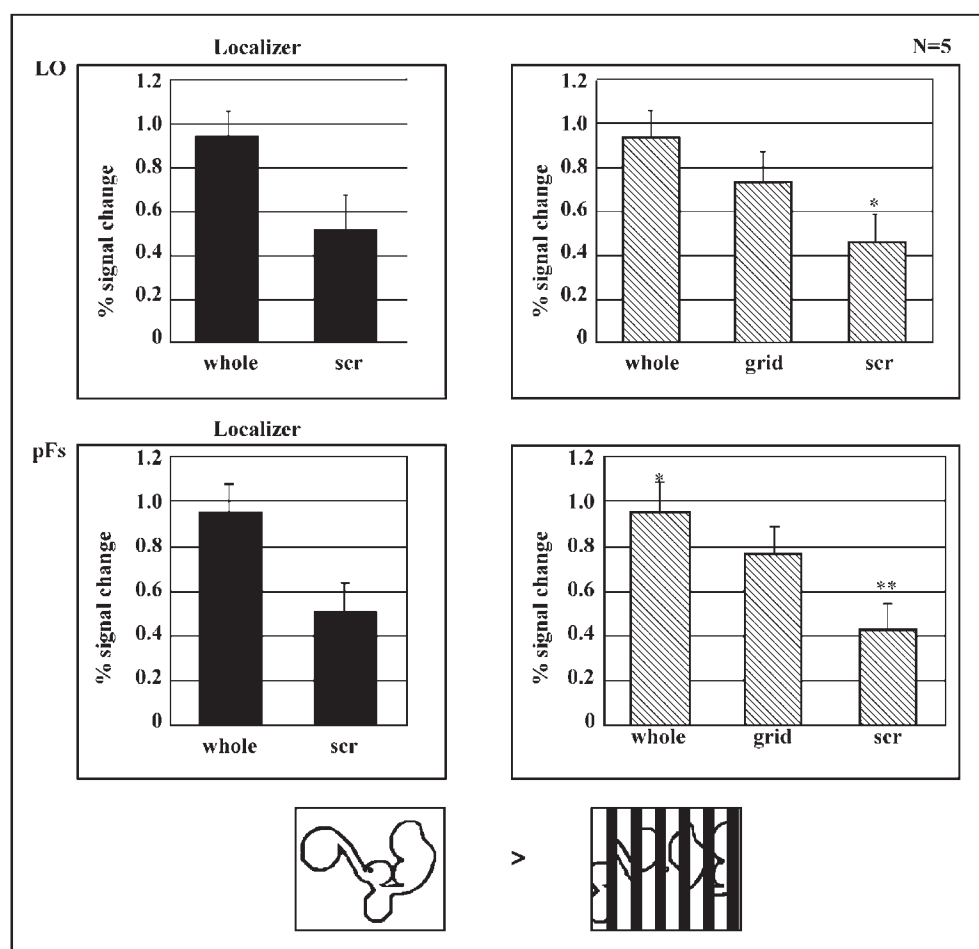


Figure 11. Completion effects for novel objects (experiment 3): activation profiles in the LOC. Histograms show the activation in LO and pFs obtained from the five subjects in the 'whole' versus 'scrambled' test in experiment 3. Epochs used in the statistical test are shown as Localizer (see Materials and Methods). The x-axis indicates the type of stimuli and the y-axis represents fMRI activation level relative to blank epochs (percentage signal change). Asterisks indicate a significant difference compared to the 'grid' condition calculated by a *t*-test (**P* < 0.05; ***P* < 0.005). Error bars specify SEM estimated across subjects.

and yet these did not affect the completion effects either. As pointed out above, the attentional demands in the one-back task are higher for the occluded objects compared to the 'whole' objects, yet the activation level was actually lower – again ruling out the possibility that the effect was due to enhanced attention.

Priming Effects

Our experimental design, which employed a large number of object images (126 images), was not optimized for the study of priming effects. In particular, as we and others have shown previously, adaptation effects are greatly minimized by the introduction of a large number of intervening object images between repetitions (Grill-Spector *et al.*, 1999; Henson *et al.*, 2000). Nevertheless, we did find a small increase in activation to the 'grid' condition when it followed a prior exposure to the 'whole' objects. This enhancement is compatible with priming effects recently reported for occluded objects (James *et al.*, 2000).

Feedback Effects

The images used in the completion experiments allow us to address another question which is of high interest; namely, to what extent activity of high-order visual areas modulates the activation in lower-order areas. In comparing the activation of low-order retinotopic areas to the 'grid' images versus the 'scrambled' images, we would expect that the bottom-up, feed-forward activation in these areas should be the same, since the local feature structure is identical in the two sets of stimuli. However, if activity in high-order visual areas contributes to the activity in early areas, we would expect the 'grid' stimuli to produce a higher activation compared to the 'scrambled' images in early retinotopic areas, since the LOC was significantly more activated by the 'grid' images. Our results did not find evidence for such feedback activation. This can be seen in Figure 5, which shows that in retinotopic areas V4 and Vp the activation to the 'grid' and 'scrambled' images was similar, or even slightly smaller to the grid compared to the scrambled condition. Furthermore, the absence of preferential activation to the 'grid' compared to the 'scrambled' images, in retinotopic areas, again supports the argument that this preferential activation is confined to high-order visual areas and does not 'trickle down' to lower, retinotopic, areas. Obviously, this conclusion is true for the specific conditions of this experiment. Other feedback effects, such as spatial and anticipatory attention effects, have been amply demonstrated in early retinotopic areas (Tootell *et al.*, 1998; Brefczynski and DeYoe, 1999; Kastner, 2000). However, our results are compatible with the notion that early areas emphasize local feature representation, while holistic completion effects are more exclusively associated with high-order object areas.

Completion Effects for Unfamiliar Objects

It could be argued that the data presented so far are unrelated to completion effects *per se*, but are driven by higher-order processes such as naming or semantic access produced by the familiar animal images. The results of our experiment 3, using unfamiliar, novel objects, rule out this interpretation. In such images, completion effects must rely on basic 'Gestalt' geometric effects, rather than semantic familiarity effects. Interestingly, the level of completion observed for familiar and unfamiliar objects was quite similar. The results further confirm the involvement of the LOC in representing both familiar and unfamiliar objects (Malach *et al.*, 1995; Kourtzi and Kanwisher, 2000b).

Notes

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