Rapid completion effects in human high-order visual areas

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Object completion is an inherent property of visual recognition in which objects can be accurately perceived in the presence of substantial obstructions. We have previously shown [Cereb. Cortex 12 (2002) 163] that high-order human object areas are driven partially by local object fragments and partially by global completion effects. Here we explored, through a backward masking paradigm, whether the balance of local and global processing is time dependent, that is, to what extent completion effects evolve at a different time compared to local image representations. In two separate experiments, subjects were presented with three types of images: (a) unobstructed line drawings of animal shapes (“whole”), (b) the same shapes obstructed by a set of parallel stripes (“grid”), and (c) a scrambled version of b in which the stripe position was shifted horizontally, disrupting the relative position of image regions but maintaining the local feature distribution (“scrambled”). Images were presented either for 60 or 250 ms followed by a mask. Both behavioral and fMRI findings from high-order occipitotemporal object areas showed consistently that object selectivity emerges at the same time as the local feature representation. Thus, object completion effects were evident at the same relative magnitude (LO: 0.5 ± 0.3 and 0.58 ± 0.04; pFX: 0.62 ± 0.3 and 0.6 ± 0.04; 60 and 250 ms, respectively) even at the short presentation durations when overall object activation was greatly reduced.

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Introduction

One of the surprising results obtained in recent fMRI studies of the human object-related cortex is the extremely wide distribution and extensive activation that is produced even by a small number of object images (e.g., see Malach et al., 2002). Such a widespread activation pattern might imply a strikingly large representation for each object image, involving perhaps hundreds of millions of neurons in each object representation. An alternative explanation for this wide activity is that due to the slow temporal resolution of the fMRI method, the activity patterns reflect a long sequence of processing stages in which both early and late visual processing events are integrated. It may be that in the early stages of the visual process, the activation does not reflect a true object-selective response, but rather a highly distributed activation to local visual elements, followed by a narrower and focused later response in which the tightly tuned object selectivity is manifested.

To resolve this issue, we have opted to use a stimulation method which allows, to some extent, to circumvent the sluggish temporal response of the fMRI method. Previously, we (Grill-Spector et al., 2000) and others (Bar et al., 2001) have shown that by presenting images at brief presentation durations using the backward masking paradigm, it is possible to interrupt the visual process in “mid flight” and follow in some detail its temporal evolvement. Here we used this approach to explore the temporal evolvement of a particularly demanding aspect of object representation—that is, object completion. To that end, we have used a set of visual stimuli containing three image manipulations: unobstructed objects, objects obstructed by parallel stripes, and the same stripes “scrambled” relative to each other (see Fig. 1). The advantage of this manipulation is that the local feature structure in the last two types of stimuli is maintained, while completion effects are disrupted.

We have shown previously (Lerner et al., 2002) that clear completion effects can be found in high-order occipitotemporal object areas. Here we followed this initial result by asking to what extent the same completion effects are manifested when image presentation time is drastically reduced.

Our results show that image completion emerges concurrently with object activation. Thus, we have failed to find cortical loci in which local nonselective feature representations appear earlier than holistic object completion effects.

Materials and methods

Experimental acquisition

Subjects were tested in a 1.5 T Signa Horizon LX 8.25 GE scanner equipped with a quadrature surface coil (Nova Medical Inc., Wakefield, MA), which allowed higher sensitivity over posterior brain regions. BOLD contrast was acquired with gradient-echo echo-planar imaging (EPI) sequence (TR = 3000, TE = 55, flip angle = 90°, field of view 24 × 24 cm², matrix size 80 × 80). Seventeen nearly axial slices, each 4 mm, with 1 mm gap between them composed the scanned volume. T1-weighted high-resolution (0.93 × 0.93 mm in-plane) anatomical images and 3D spoiled gradient echo sequence (0.93 × 0.93 × 1.2 mm) were obtained on each participant. Using anatomical data, precise
cortical segmentation, reconstruction, and volume-based statistical analysis were done for each subject.

Subjects

Fourteen normal subjects participated in the study (10 subjects in the first experiment, seven subjects in the second experiment, and three subjects in both). The age range was 25 to 52 years; six were male, two left-handed, none had an abnormal neurological history. Each subject signed a consent form approved by the Tel Aviv Sourasky Medical Center.

Stimuli

All visual stimuli were generated on a PC, presented via an LCD projector (Epson MP 7200) onto a translucent screen, and shown in a mirror positioned approximately 45° above the subject’s forehead. A red fixation point was presented throughout all the experiments.

Experiment 1

Visual stimuli (126 images, size 14° × 12°) were obtained from several commercial databases and adapted using Adobe Photoshop 6.0 software package (Adobe Systems Incorporated). The experiment included two different stimulus conditions—“grid” and “scrambled”—each presented for two exposure durations—60 and 250 ms. In the “grid” condition, line drawings of animal shapes were occluded by vertical green bands (1.2° × 12°); in the “scrambled” condition, images were constructed by randomizing the relative position of the “object stripes”—that is, the stripes in-between the green obstructing stripes (Fig. 1, top). The experiment lasted 444 s, a block design paradigm was used—stimulus epochs (9 s) were interchanged with blank epochs (6 s, the first and the last blanks were longer). Each scan consisted of 28 epochs composed of 18 different stimuli followed by a mask. The masks were created from the image itself following a scrambling filter—each image was broken into squares (0.6° × 0.6°), which were then randomly scrambled. We made sure that for presentation duration of 20 ms, images followed by a mask were not recognizable. The masks supplemented the presentation duration to 500 ms—that is, 440-ms mask for the 60-ms image and 250-ms mask for the 250-ms image. The schematic representation of the temporal sequence is illustrated in Fig. 1 (bottom). In all epoch types, the subjects were asked to covertly name the objects or to guess if they could not recognize the images.

Experiment 2

This experiment was a modified version of the previous one. It had similar experimental configuration, but this time the same line-drawings of animal shapes without occlusions (“whole” condition) were contrasted with the “grid” stimuli, again for two rates—60 and 250 ms (Fig. 6). “Scrambled” stimuli were used in the experiment as a localizer only for one exposure—250 ms. Again, a mask supplemented each image up to 500 ms. It should be noted that in this experiment, in the “grid” condition, the stripes were overlaid on the mask as well. The experiment lasted 549 s and consisted of 35 visual epochs interleaved with blanks.

Psychophysical performance

Psychophysical performance was evaluated for each subject about 3 weeks after the fMRI scan. This rather long period was chosen to minimize possible priming or memory effects due to the prior exposure to the images during the fMRI scans. Subjects were requested to overtly name the animal at the basic category level—for example, a “cat”, a “cow”. Same naming task was used in all conditions including the “scrambled” condition. Percentage of correct naming was used for the performance estimation. The stimuli were shown in the same order as during the fMRI scan; however, the blanks were extended up to 1500 ms to give subjects sufficient time for overt naming of each object. The procedure was of a “forced-choice” design, that is, subjects were asked to guess the most likely animal shape they thought they saw even when they were not sure. Note that due to the many possible alternative names, the use of two-alternative statistics is inappropriate. However, the “forced-choice” design eliminates the personal bias factor, and since random guessing is unlikely to produce correct responses, the percent correct measure reduces to a sensitivity measure analogous to d'.

Data analysis

The fMRI data were examined using the “BrainVoyager” software package (Brain Innovation, Masstricht, Netherlands) and complementary in-house software. Detailed anatomical maps were obtained for each subject using a 3D-spoiled gradient echo scan. The cortex reconstruction included the segmentation of the white matter with a grow-region function, the smooth covering of a sphere around the segmented region, and the expansion of the reconstructed white matter into the gray matter. Following surface reconstruction, the brain was inflated to allow viewing of sulcal cortex and unfolded into the flattened format by introducing cuts along the calcarine sulcus.

Statistical analysis was based on the general linear model (GLM) (Friston et al., 1995). Each experimental condition (except for blanks) was defined as a separate predictor, and a box-car shape was used for each predictor. The analysis was performed independently for the time course of each individual voxel for each subject. An average time-course was calculated from all voxels within a priori defined regions of interest (ROI). Only voxels with correlation value larger than 0.2 (P < 10⁻⁵, uncorrected) were used in the statistical analysis. To create the two-color maps, the GLM model was recalculated using a subset of the predictors. To show the relative contribution of two functional responses, the color coding was used to symbolize the relative contribution of each category—the darkest color (green or red) represents exclusive contribution of one predictor set over the other and the colors between these extremes depend on the level of contributions of each predictor set.

Individual subject analysis

This procedure included motion correction and high-frequency temporal filtering. In each functional scan, the first three images were removed and a hemodynamic response delay of 3 s was assumed. 2D functional activation superimposed on the corresponding 2D anatomical slices was incorporated into the 3D data through trilinear interpolation and transformed into Talairach space (Talairach and Tournoux, 1988). Finally, unfolded cortical surfaces with overlaid fMRI activation were obtained.
Multisubject analysis

In addition to subject-by-subject analysis, data were analyzed in a multisubject random effect approach. For this purpose, the time series of images of all subjects were converted into Talairach space and z-normalized. Then, for each subject, the relative contributions of the predictors for each contrast were estimated separately, and from the obtained set of values (one mean value and variance for subject), the significance at the multisubject level (random effect) was computed. The multisubject functional maps were superimposed on an inflated or unfolded Talairach normalized brain of one subject. Statistical level ranged from $P < 0.05$ (darker colors) up to $P < 0.001$ (brighter colors) and was indicated by the color scales.

“Internal localizer” procedure

Details of the approach were previously published (Lerner et al., 2002). Briefly, one subset of the epochs of each condition was used to localize the ROI, while another subset of the same condition, not included in the localization test, was used to evaluate the activation level. This procedure allowed us to measure the activation level and conduct the statistical localization test in the same scan, thus reducing discrepancies between scans due to head motion. The average activation obtained from epochs, which were used for localization, is labeled as “localizer” in the figures (Fig. 8). The ROI was defined for each subject separately; the collected time series from epochs that were not taken in the localization test were averaged within each subject and then averaged across all subjects. The results are shown in graphs separately.

Borders of retinotopic visual areas

The representation of vertical and horizontal visual field meridians (Sereno et al., 1995) was mapped in the subjects to establish the borders of retinotopic visual areas (DeYoe et al., 1996; Tootell et al., 1996). The procedure is described by Grill-Spector et al., 1998a. Briefly, visual stimuli consisted of triangular wedges were presented either vertically (upper or lower) or horizontally (left or right) and 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 center cross.

Results

Recently we reported that cortical activation associated with object completion effects was mainly observed in high-order object-related areas (Lerner et al., 2002). In the present study, we aimed to explore whether the completion effects in these areas may evolve at a different time scale compared to local feature representations.

One possibility to explore this issue is to focus on the “grid” and “scrambled” conditions. Here the completion effect is manifested by an increased activation during the “grid” compared to “scrambled” conditions. We studied the temporal evolution of this effect by interrupting visual processing using the backward mask. To that end, we conducted Experiment 1 in which subjects viewed either line drawings of animals with superimposed green vertical bars followed by a mask (“grid”, Fig. 1, left) or the same images with the randomly scrambled object-containing bands also followed by a mask (“scrambled”, Fig. 1, right). Each set of visual stimuli was shown for 60 and 250 ms (see Materials and methods for more details).

The duration of 60 ms was chosen based on a preliminary psychophysical experiment in which subjects were required to identify images presented for 20, 40, 60, 120, and 250 ms. Sixty milliseconds was found to be the minimal time required for recognition. According to Rauschenberger and Yantis (2001), as well as our previous work (Lerner et al., 2002), 250-ms duration was sufficient for a full manifestation of completion effects, so it was taken as the longer exposure during the fMRI experiments.

Among possible results, two extreme outcomes can be envisioned. One possibility is that the completion processes are much slower to evolve compared to the local feature activations. In that case, we would expect that for the 60-ms presentations, the completion effects will be weak, and consequently, we will find only a slight difference between the activation levels of the “grid” and “scrambled” conditions; whereas for the 250-ms duration, as the delayed completion effects “kick in,” the difference (i.e., activity related to the completion effect) will be greatly accentuated.

An alternative possibility is that the emergence of completion effects is as rapid as the local feature representation. In that case, we would expect the same level of preferential “grid” activation to be observed both for the short 60-ms exposure and for the longer 250-ms exposures.

Recognition performance under short and long exposure durations

We first present the results of the behavioral tests. The behavioral results obtained for 10 subjects are presented in Fig. 2a. As can be seen, recognition performance was substantially higher with the longer presentation time, indicating that 60-ms exposure was effective in disrupting recognition processes. However, despite this...
Fig. 1.

Fig. 3.
Fig. 6. Examples of stimuli used in Experiment 2. Three types of stimuli were used in the experiment: line drawings of animal shapes without occlusion ("whole" condition), "grid" stimuli, and "scrambled" ones. "Whole" and "grid" conditions were presented for two exposure durations—60 and 250 ms. "Scrambled" images were used for ROI localization (see Material and methods). An interleaved short-epoch design was used. Each stimulus was followed by a mask, which supplemented the presentation duration to 500 ms. The schematic representation of the temporal sequence is illustrated in the bottom.
significant difference in recognition level, for both exposure durations, object recognition during the “grid” condition was significantly superior to recognition of the “scrambled” images and the ratio “scrambled” or “grid” was not significantly different for the two exposure durations (Fig. 2b). Note that since no estimate was made for the guessing probability, the results may reflect only an upper bound estimate on the percentage of correct response.

Visual activation under short and long exposure durations

We looked for completion effects in each subject by contrasting the activation in the “grid” and “scrambled” epochs for the two stimulus durations (Fig. 3a). For this purpose, we superimposed two activation maps obtained in the test “grid” vs. “scrambled”: one for 60 ms (magenta) and one for 250 ms (cyan). Fig. 3b shows the results of such analysis on a multisubject map (n = 10, random effect). The retinotopic regions were localized based on anatomical and functional criteria by mapping the representation of the visual field meridians in each subject (white dotted lines) (DeYoe et al., 1996; Grill-Spector et al., 1998b; Sereno et al., 1995; Tootell et al., 1996). It can be seen that regions showing preferential activation to the “grid” over “scrambled” conditions for 60- and 250-ms presentations extensively overlapped (blue) in occipitotemporal object-related regions—particularly, in the broad ventral occipitotemporal (VOT) region, which extends from the collateral sulcus (CoS) medially to the occipitotemporal sulcus laterally and includes the posterior fusiform gyrus (pFs) (Malach et al., 2002), and the more dorsally located lateral occipital region (LO) located at the posterior part of the inferior-temporal sulcus (Grill-Spector et al., 1999).

Interestingly, retinotopic regions were somewhat more activated for 60-ms object images followed by mask. Cortical activation for 250-ms images for the same threshold appeared slightly anterior and dorsal to those activated by 60-ms exposures.

To obtain a quantitative measure of the activity level during the different experimental conditions, we searched for regions that were more activated by “grid” images compared to “scrambled” ones, irrespective of presentation duration, and performed time course analysis by sampling from three previously defined regions—LO, pFs, and CoS, indicated by circles on a two-color average map superimposed on the inflated brain of a single subject (Fig. 4c). Fig. 4a demonstrates the results of this analysis. Note that the activations during the “grid” and “scrambled” epochs were measured independently from epochs not included in the statistical tests.

As can be seen, LO and pFs showed significant preferential activation to the “grid” stimuli compared to the “scrambled” ones both for 60- and 250-ms presentations (ANOVA: two-factor with replication: LO: a main effect of duration: $P < 10^{-10}$; a main effect of condition: $P < 0.0005$; no significant interactions: $P = 0.1$; pFs: a main effect of duration: $P < 10^{-6}$; a main effect of condition: $P < 0.0005$; no significant interactions: $P = 0.2$. One-tailed paired $t$ test: $P < 0.0005$ in both cases). It should be noted that the activation significantly decreased for the shorter (60 ms) duration (red stars, Fig. 4a), indicating that at this duration, object activation was close to its threshold. Nevertheless, the activation ratios between the preferred and nonpreferred conditions measured for each duration were similar for 60- and 250-ms durations: LO: $0.5 \pm 0.3$ and $0.58 \pm 0.04$, respectively; pFs: $0.6 \pm 0.3$ and $0.59 \pm 0.04$, respectively (Fig. 4b). Thus, it appears that completion effects emerge as rapidly as local image representations, even at the duration close to activation threshold. Note that CoS shows a weaker, albeit statistically significant (ANOVA: two-factor with replication: a main effect of duration: $P < 0.005$; no significant effect of condition: $P = 0.4$; no significant interactions: $P = 0.9$). One-tailed paired $t$ test: $P < 0.005$ for 60 ms and $P < 0.05$ for 250 ms) completion effect compared to LO and pFs.

It was interesting to compare this pattern of activation to the activity in early retinotopic visual areas. The results of this analysis are shown in Fig. 5a. Two main effects can be observed in the activation patterns: First, in contrast to high-order object-related areas, early visual areas did not show a significant preferential activation to the “grid” stimuli for either duration, although a beginning of such selectivity could be observed in area V4. This is compatible with our previous findings showing that these areas do not show object selectivity (Grill-Spector et al., 1998b; Lerner et al., 2001). On the other hand, a clear duration effect was increasingly evident at progressively higher
order areas so that in V1, activation was quite similar for the short and long durations (ANOVA: two-factor with replication: no significant effects of condition or duration: $P = 0.6$ and 0.3, respectively; no significant interactions: $P = 0.7$); while in V3A and V4, there was more activation for the 250-ms exposure compared to the 60 ms (ANOVA: two-factor with replication: V3A: a main effect of duration: $P < 10^{-5}$; no significant effect of condition: $P = 0.8$; no significant interactions: $P = 0.4$; V4: a main effect of duration: $P < 10^{-5}$; no significant effect of condition: $P = 0.3$; no significant interactions: $P = 0.6$). One-tailed paired $t$ test: V3A: $P < 0.10^{-5}$, V4: $P < 10^{-5}$). This effect is illustrated in Fig. 5b, which shows the “temporal index” calculated as the ratio 60:250 ms for each condition in all retinotopic visual areas. Note that in V1 activation was almost similar for the short and long durations whereas at the progressively higher areas there was more activation for the 250-ms exposure compared to the 60 ms.

Fig. 5. Activation profiles in retinotopic visual areas. (a) Graphs show the average activation ($N = 10$) derived from the retinotopic regions V1, V2, VP, V3, V4, and V3A defined by retinotopic mapping and overall visual activation to the test stimuli. The $x$-axis denotes the type of stimuli and the $y$-axis shows the percent signal change calculated relative to blank epochs. Note that in contrast to high-order object areas, early visual areas did not show a significant preferential activation to the “grid” stimuli for either duration. However, there was a significant effect of stimulus exposure duration. Asterisks indicate significant difference between exposure durations (*$P < 0.05$; **$P < 0.005$; ***$P < 10^{-5}$; one-tailed paired $t$ test). (b) The exposure duration effect was quantified as the “temporal index” calculated as the ratio 60:250 ms for each condition in all retinotopic visual areas. The icons above the graphs illustrate the presented stimulus type. Note that in V1 activation was almost similar for the short and long durations whereas at the progressively higher areas there was more activation for the 250-ms exposure compared to the 60 ms.
Experiment 2

Another alternative for studying the relative dynamics of local and global representations is to focus on the image “complexity” effect—that is, the enhanced activation to the “whole” unobstructed images compared to the “grid.” One possibility is that such enhanced activation might be due to the richer or more diverse set of local features, which are present in the “whole” images compared to the “grid” where about half of the local object features are obstructed. Thus, such enhanced activation might reflect a failure of completion mechanisms to “fill in” the missing object elements. To explore this alternative, we conducted a second experiment (see Fig. 6) in which the same objects were presented either without occlusion (“whole” condition) or with the “grid” condition, again using 60- and 250-ms exposures. “Scrambled” images were used in this experiment for ROI localization only (see Material and methods). In this experiment, it is expected that slow-completion effects might be manifested as a large difference between the “whole” and “grid” conditions for the short exposure duration. This “complexity” effect should decline as completion effects start playing a dominant role in the longer duration.

The results of comparing the activation to “whole” vs. “scrambled” conditions are shown on unfolded and inflated brains (Fig. 7). As can be seen here and in agreement with our previous results, almost the same cortical regions were activated by “whole” and by “grid” stimuli—again regions most sensitive to completion effects are denoted by circles. LO, lateral occipital; pFs, posterior fusiform gyrus; CoS, collateral sulcus; VOT, ventral occipitotemporal region; A, anterior; P, posterior.

Fig. 7. Preferential object activation—multisubject map. Average functional activation maps ($N = 7$) showing relative activation to “whole” vs. “scrambled” images superimposed on the left (L) and right (R) hemispheres of the inflated and unfolded cortical surfaces of a single subject. The maps were constructed using random effect GLM statistical analyses, with preferential activation to “whole” epochs shown in green, compared to “scrambled” shown in red. Yellow and orange colors specify more balanced activation levels. The anterior border of retinotopic areas is denoted by red dotted lines. Note the large overlap in cortical regions activated by the “whole” and by the “grid” stimuli. Regions most sensitive to completion effects are denoted by circles. LO, lateral occipital; pFs, posterior fusiform gyrus; CoS, collateral sulcus; VOT, ventral occipitotemporal region; A, anterior; P, posterior.

The level of the completion effect was estimated, as in the previous experiment, by analyzing time course of activation from the selected regions. The results of this analysis are shown in Fig. 8a. Again, we sampled from the regions of interest according to their preferential activation to the “whole” condition compared to the “scrambled” condition. Note that the results were similar to those obtained in the previous experiment (see Fig. 4 for comparison) although the overall signal was lower. Similar to Experiment 1, reducing the exposure duration to 60 ms resulted in a significant reduction in activation to the “whole” condition, confirming that for this short duration, visual processing was significantly affected.
by the masking procedure. Inspecting the “complexity” effect, that is, the difference between the “whole” and “grid” conditions, we observed a slight trend for enhancement for the longer exposure time: LO: 0.8 ± 0.2 and 0.9 ± 0.2 for 60 and 250 ms, respectively; pFs: 0.76 ± 0.29 and 0.85 ± 0.09 for 60 and 250 ms, respectively (Fig. 8b). However, this difference was not significant across subjects.

Interestingly, the CoS did not manifest a significant difference between the “whole” and “grid” conditions, most likely due to higher sensitivity in this region to the obstructing stripes.

Behavioral data obtained in Experiment 2 from seven subjects are shown in Fig. 9a. Again, recognition results of the subjects significantly improved with increasing presentation time, and for both durations, correct naming of the “whole” images was signif-

Fig. 8. Activation profiles in high-order visual areas—Experiment 2. (a) Graphs depicting the activation profiles for the lateral occipital, posterior fusiform, and collateral sulcus regions obtained from seven subjects in the “whole” vs. “scrambled” test. 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 levels relative to blank epochs (percentage of signal change). Asterisks indicate a significant difference for each exposure duration computed by a one-tailed paired t test (*P < 0.05). Error bars specify ±SEM estimated across subjects. (b) Activation ratios between the preferred (“whole”) and nonpreferred (“grid”) conditions measured for 60- and 250-ms durations in the lateral occipital and posterior fusiform regions.
The results from the behavioral measurements were largely compatible with the fMRI results—thus, shortening the exposure times indeed lowered both the fMRI activation and recognition performance, indicating that at these short times the neuronal processes became disrupted. Such correlation between fMRI signal strength and recognition performance has been amply documented previously (Bar et al., 2001; Grill-Spector et al., 2000). However, the preferential recognition in the “grid” condition compared to the “scrambled” one was quite similar—further indicating that completion effects can be observed behaviorally as early as for 60-ms duration. The behavioral findings of Experiment 2 did show some enhancement in the advantage for the “whole” compared to the “grid” position for the short 60-ms duration (see Fig. 9). Thus, there was some discrepancy between the behavioral results and the fMRI activations observed in this experiment, although a similar trend was observed between the two measures. The source of this discrepancy is not clear—one possibility is that it may reflect a “ceiling” effect in the recognition performance, which approached 100% for the whole images.

The results of the present study thus argue against the interpretation that the wide distribution of activity in high-order object-related areas is generated by a fairly slow multistage process by which a distributed pattern of nonselective local-feature representations gets trimmed into small foci of more tightly tuned holistic representations. Rather, the results support the notion that the holistic representation emerges as such right from the earliest stages of visual activation. The finding that holistic processes occur extremely rapidly is compatible with the work of Grill-Spector (2003) who found, using both psychophysics and event-related fMRI, that object recognition and detection occur at similar time scales.

However, our results do not address the possibility that the sharpness of holistic shape tuning might have a slow dynamics, that is, it could be that the representations manifest completion effects right from the start but are initially broadly tuned shape-wise and only later become more sharply tuned to specific object templates. This issue will require a further study to clarify.

Concerning the various object-related regions, we found no significant difference in completion effects between the more
dorsal LO and more ventral pFs. This result is compatible with our previous work on completion effects and also compatible with a substantial literature demonstrating clear holistic effects also in the more dorsal object-related cortex (Hasson et al., 2001; Kourtzi and Kanwisher, 2001; Kovacs et al., 1995).

The results show an interesting functional distinction between the more medial CoS and the laterally located pFs, in that the CoS manifested a weaker level of completion effect (i.e., smaller enhancement of the “grid” vs. “scrambled” condition). Previous studies showed a clear object-related dissociation between these two regions in that the pFs showed a preferential activation to face images (Haxby et al., 2000; Kanwisher et al., 1997; McCarthy et al., 1997; Tong et al., 2000), while the CoS was preferentially activated to building and scene images (Aguirre et al., 1998; Epstein and Kanwisher, 1998; Ishai et al., 1999). It is not clear at present whether the apparent lack of completion effects in the CoS might be a general effect, which may be due to different computations that are performed in this region (e.g., large scale integration, orientation in space, etc.), or whether this was due to a more specific object-related effect, that is, the choice of animal images that might not be the optimal stimuli for this region.

Regarding early visual areas, the main observed effect was a trend for enhanced activation for the longer target exposure times at progressively higher areas. This progressive increase is suggestive of a hierarchical sequence (Lerner et al., 2001); however, the functional source of this effect is not clear. Recalling that a main parameter that changes with increasing duration is a relatively longer exposure to the obstructing gratings stimuli, one could conceive of two alternative explanations for the gradual increase along the hierarchy of visual areas: First, it might reflect a progressively increased stimulus sensitivity to the large gratings. Second, it may reflect a progressively increased “sluggishness” of processing at higher retinotopic areas so that longer exposures are required to fully reveal the grating-sensitivity of these areas. Further experiments will be required to distinguish between these alternatives.

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