Vase or Face? A Neural Correlate of Shape-Selective Grouping Processes in the Human Brain

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Abstract

■ Recent neuroimaging studies have described a differential activation pattern associated with specific object images (e.g., face-related and building-related activation) in human occipito-temporal cortex. However, it is as yet unclear to what extent this selectivity is due to differences in the statistics of local object features present in the different object categories, and to what extent it reflects holistic grouping processes operating across the entire object image. To resolve this question it is essential to use images in which identical sets of local features elicit the perception of different object categories. The classic Rubin vase–face illusion provides an excellent experimental set to test this question. In the illusion, the same local contours lead to the perception of different objects (vase or face). Here we employed a modified Rubin vase–face illusion to explore to what extent the activation in face-related regions is attributable to the presence of local face features, or is due to a more holistic grouping process that involves the entire face figure. Biasing cues (gratings and color) were used to control the perceptual state of the observer. We found enhanced activation in face-related regions during the "face profile" perceptual state compared to the "vase" perceptual state. Control images ruled out the involvement of the biasing cues in the effect. Thus, object-selective activation in human face-related regions entails global grouping processes that go beyond the local processing of stimulus features. ■

INTRODUCTION

Neural analysis of the visual scene in early visual areas is inherently local. The receptive fields of neurons in these areas are relatively small and sensitive to local edges and contours. Yet visual perception of objects is global and unified. This transformation requires grouping processes by which local features have to be "assigned" to a particular figure (e.g., Ullman, 1996; Marr, 1982). Surprisingly little physiological evidence has been obtained that directly explores the neural correlates of such perceptual phenomena (but see recent single-unit recording works by Zhou, Friedman, & von Der Heydt, 2000; Lee, Mumford, Romero, & Lamme, 1998; Zipser, Lamme & Schiller, 1996; Lamme, 1995).

Recently, a substantial number of neuroimaging studies have found that human lateral occipital and occipito-temporal cortex is sensitive to images of objects compared to a variety of textures and noise patterns (Kourtzi & Kanwisher, 2000a; Grill-Spector et al., 1999; Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999; Malach et al., 1995). Furthermore, subdivisions of occipito-temporal cortex have been reported to show segregation according to specific object categories. Prominent examples are areas selective for faces (Haxby, Hoffman, & Gobbini, 2000; Tong, Nakayama, Moscovitch, Weinrib, & Kanwisher, 2000; Halgren et al., 1999; Kanwisher, Chun, McDermott, & Ledden, 1996) and buildings (Aguirre, Zarahn, & D'Esposito, 1998; Epstein & Kanwisher, 1998) as well as other object categories (Ishai et al., 1999). It is generally assumed that such category-specific organization necessarily implies a holistic representation that goes beyond local features. Indeed, high-order object representations do show remarkably abstract characteristics such as substantial size and position invariance (Grill-Spector et al., 1999), and invariance to the visual cues used to define objects (Gilaie Dotan, Ullman, Kushnir, Steinberg, & Malach, 2000; Kourtzi & Kanwisher, 2000a; Grill-Spector, Kushnir, Edelman, Itzchak, & Malach, 1998).

Nevertheless, selective activation to one set of objects relative to another can still be explained by differences in the distribution of local object elements or features. To appreciate this point, consider a small aperture that samples local parts of an object, such as a tumbler or a face (Figure 1A and B). It is rather straightforward to see that although the sampling from the two images is strictly local, the aggregate distributions of local object features that can be obtained from the two object categories are substantially different and thus could provide the basis for the observed object selectivity. This possibility is compatible with evidence

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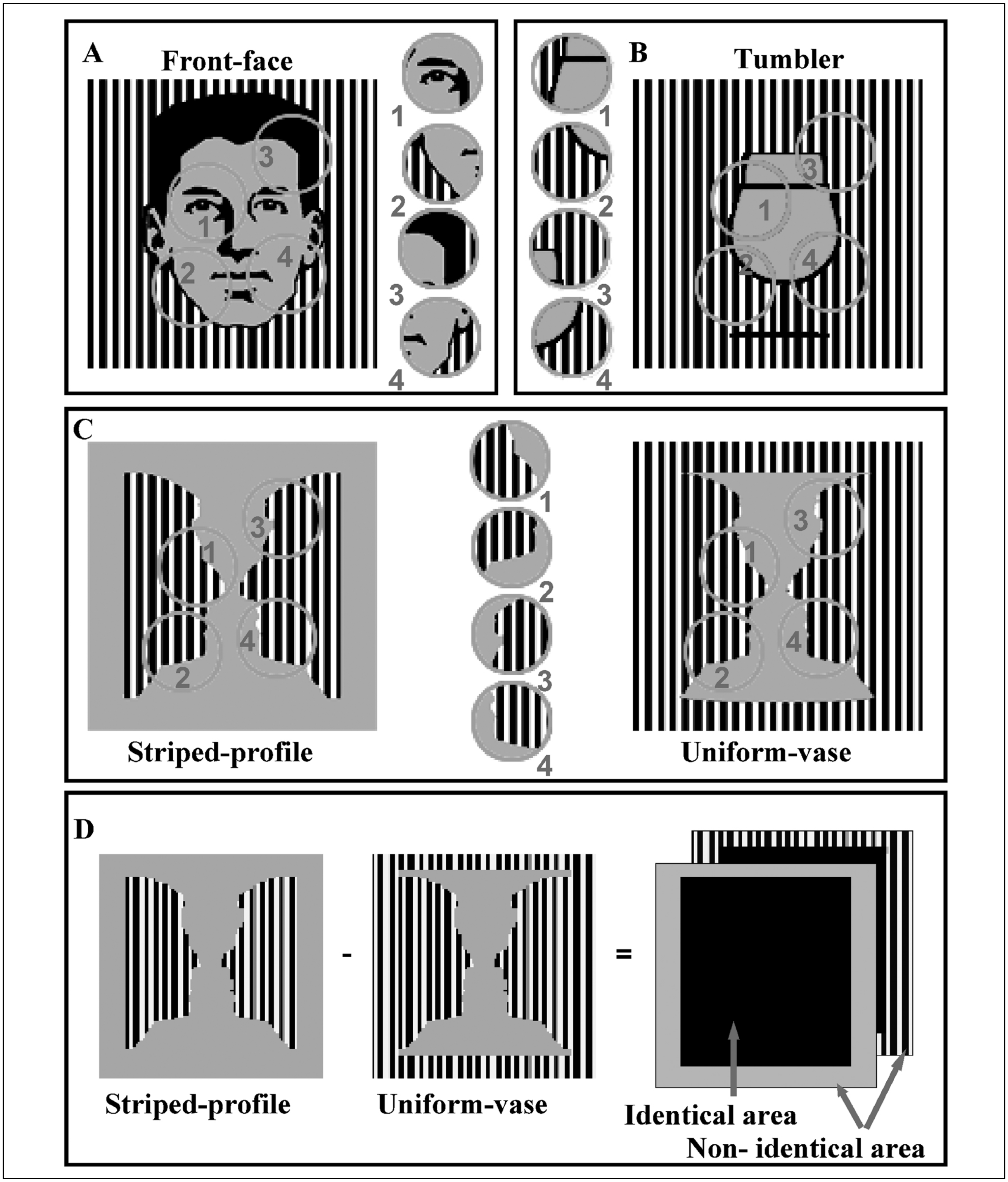

Figure 1. Local feature content of visual images used in the experiment. Types of drawings of a front face (A), a tumbler (B), and Rubin vase–profile (C, right and left side, respectively) used in the experiment. The circles on each image represent four placements of a hypothetical aperture, which samples a local part of the image. As can be seen the aggregate distributions of local object features that is obtained from the front face (A) and the tumbler (B) is substantially different (numbered circles in columns), and could underlie the shape selectivity found for these images. In contrast, the aggregate distributions of local object features in the striped-profiles and uniform-vase images (C) is similar since the vast majority of local features is identical in the two images (middle column of circles). Thus, it could serve as a model system to dissociate between holistic and local features representation. (D) The feature difference between the striped-profiles and uniform-vase images obtained by subtracting one from the other. The black box in the center of the squares on the right represents the area that is identical in the two images. The outer uniform or striped frames represent the nonidentical area. This slight change in the surround frame (uniform color or striped frame) induces a closure effect, which produces the marked shift in perceptual state between the vase and the profile.

of selectivity for ''moderately complex'' visual features obtained from single cells recorded in the inferior temporal (IT) cortex of the monkey (Tanaka, Saito, Fukada, & Moriya, 1991; Tanaka, 1996). Even when the shape-selective activation shows a high degree of cue invariance and abstraction (Kourtzi & Kanwisher, 2000a; Grill-Spector, Kushnir, Edelman et al., 1998; Grill-Spector et al., 1999) it might still result from activation induced by local object features. For example, the preferential activation to motion-defined object shapes may be produced by a set of features, which are delineated by local motion cues. Thus, high-level and abstract representations do not necessarily imply global grouping processes.

One way to assess the involvement of global grouping processes that go beyond the local feature representation is to use images whose local feature structure is nearly identical, yet they elicit perceptions of different object categories. A step in that direction was accomplished with the demonstration that illusory ''Kanizsa'' figures produce significant activation in high-order object areas (Mendola, Dale, Fischl, Liu, & Tootell, 1999). Such figures depend on subtle changes in local feature arrangements that cannot, by themselves, explain the observed activation. However, no attempt was made to correlate this activation pattern with category-selective organization, so its role in determining such selectivity remains unclear.

Perhaps the best-known example that could highlight category-specific holistic processing is the classic Rubin vase–face illusion. In this illusion, the same local contours create two different visual percepts, depending on whether the contours are ''assigned'' as figure border to the peripheral surfaces (which consequently appear as two profiles), or to the center surface (which appears as a vase). In the present study, we employed a modified Rubin vase–face illusion to explore to what extent the activation in face-related regions is attributable to the presence of local face features, or is the result of a more holistic grouping process that involves the entire face figure (Figure 1C). Note that in this modified Rubin illusion, sampling the image with a local aperture will give nearly identical feature sets since the vast majority of the local features are identical in the two images. It is a slight change in the surround frame (uniform color or striped frame) that induces the marked shift in perceptual state between the vase and the face profile (Figure 1D).

Thus, if local features mediate face-selective activation, we will expect that activation in face-related regions will be similar in the ''vase'' and ''face profile'' conditions since the local feature structure is similar in the two images. In contrast, if global processes, which go beyond the local contours, drive the face-related activation, we will predict higher activation in these regions to the ''face profile'' perceptual state compared to the ''vase'' perceptual state. Our results reveal a clear modulation of fMRI activation depending on whether the object contour was perceived as the face profiles or vase. Thus, our study shows that face-related activation in the occipitotemporal cortex is modulated by global grouping processes involved in assigning the local features to the face-profile surface, and is not induced solely by representation of local stimulus features.

RESULTS

A major obstacle in using the classic version of the bistable Rubin vase–face illusion for fMRI study is that the transition between the perceptual states is quite fast, and often difficult to determine. To overcome this difficulty we modified the illusion by biasing the perception to one state or the other. The biasing was accomplished in two ways: (a) by coloring one object in a uniform color (uniform vase or uniform profile) and placing it over a striped background, (b) by closure of the striped-profile regions and placing them over the uniform-color background (Figure 2B). In order to prevent subjects from seeing the complementary perceptual interpretation each figure was presented for 200 msec, and was followed by a masking grid that remained on the screen for 800 msec (Figure 2C). To assess subject's perception we ran a psychophysical test outside the magnet using the same stimuli and presentation setting. All six subjects reported seeing the figure at the intended perceptual state, and rarely being aware of the complementary perceptual interpretation [96 ± 4% (*SD*), correct responses]. The crucial point to note is that the majority of the local features in the striped profiles and the uniform vase are identical. This is illustrated in Figure 1D, which shows a subtracted image of the striped profiles and the uniform vase images. Note that except for a narrow uniform frame surrounding the striped profiles, the two images are identical, yet they elicit markedly different percepts.

To independently localize face-related regions we included drawings of front faces, which were contrasted with tumbler images, since it was shown that both front-face and profile stimuli activate face-related regions (Tong et al., 2000). Finally, to control for differences in attentional shift to the central and peripheral stimuli, the tumbler images were presented in two conditions: either one tumbler presented centrally (similar to the vase) or two tumblers presented more peripherally (similar to the profiles). The experiment was run in two versions, using the same localizer and vase images but with striped profiles in Experiment 1 and uniform profiles in Experiment 2 (Figure 2).

Holistic versus Local Processing in Face-Related Regions

Our analysis started with the localization of brain regions that were preferentially activated by front-face images

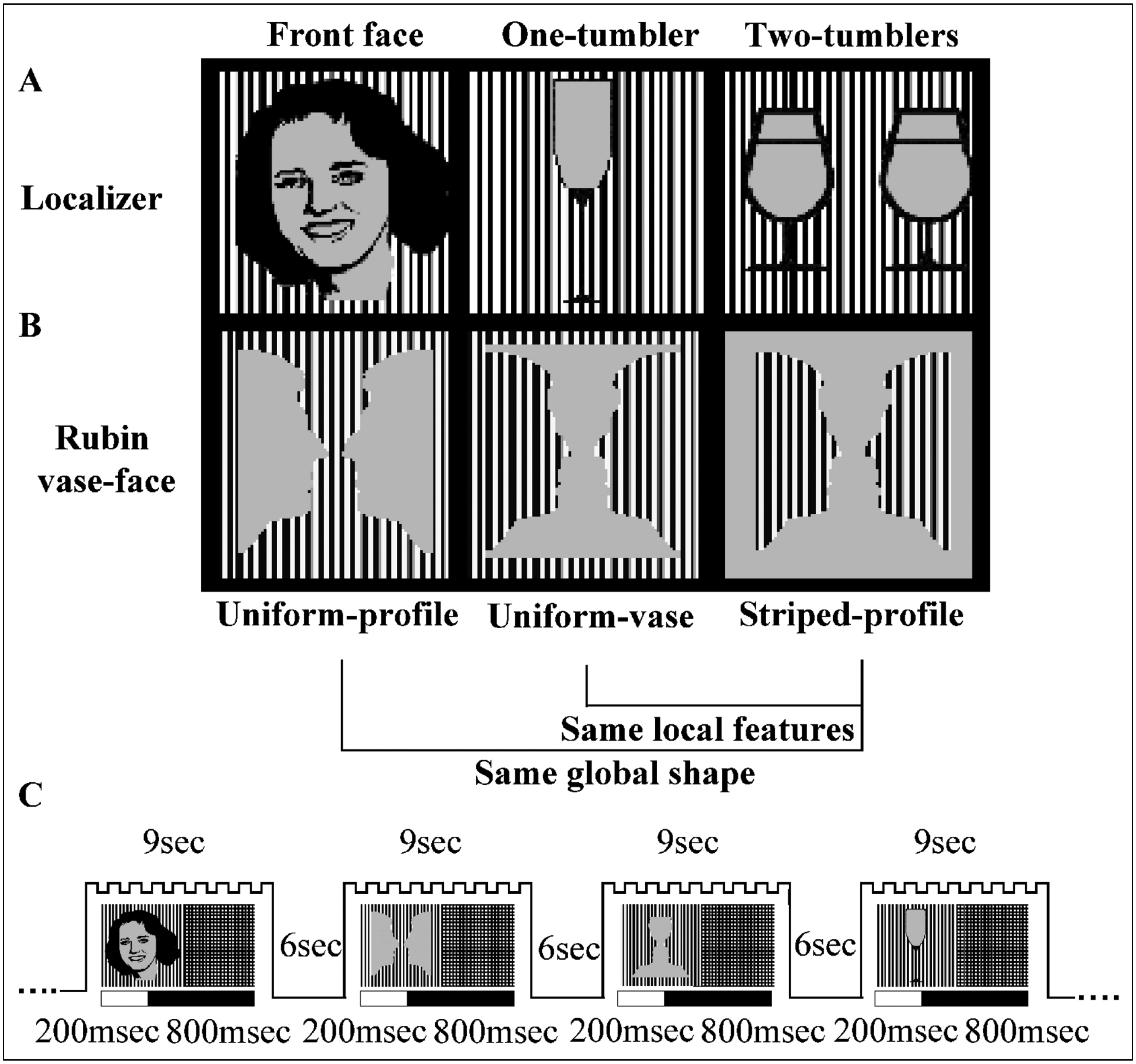

Figure 2. Experimental design. (A) Localizer images: To independently localize face-related regions we included line drawings of front face, which were contrasted with tumbler images. The tumbler images were presented in two conditions: either one tumbler presented centrally (similar to the vase) or two tumblers presented more peripherally (similar to the profiles), to control for attentional effects. (B) To reveal holistic aspects of face activation we employed a modified version of the Rubin vase–face illusion (see Results and Figure 1). The images included a uniform color vase and striped profiles (Experiment 1) or a uniform color vase and uniform color profiles (Experiment 2). Note that the uniform vase and striped profiles have similar local features, while the striped profiles and uniform profiles differ in their local features but have similar global shape. (C) An interleaved-blocked presentation design was used in the experiment. Each epoch lasted 9 sec, followed by a 6-sec blank. Nine images of the same type were presented in each epoch. Each image was presented for brief time, 200 msec, and was followed by 800 msec masking grid to prevent subjects from seeing the complementary perceptual interpretation.

compared to tumbler images. In all subjects, and in agreement with previous studies, face-related voxels were found in the posterior fusiform gyrus and in the lateral occipital region (red–yellow in Figure 3). The Talairach coordinates of the front-face-selective regions are: fusiform gyrus: right, 36 ± 4 (*SD*), −46 ± 6, −16 ± 4, left, −36 ± 5, −48 ± 9, −19 ± 4; lateral occipital cortex: right, 38 ± 6, −72 ± 6, −10 ± 4, left, −43 ± 6, −75 ± 6, −10 ± 10. Preferential activation for tumbler images compared to front-face images (blue in Figure 3) was observed in a more dorsal focus within the occipito-temporal cortex and in a medial region in the collateral sulcus.

To examine the effect of holistic versus local processing on the activation in the face-related regions identified above, we compared the MR signal during the "profiles" and "vase" perceptual states. The mean MR

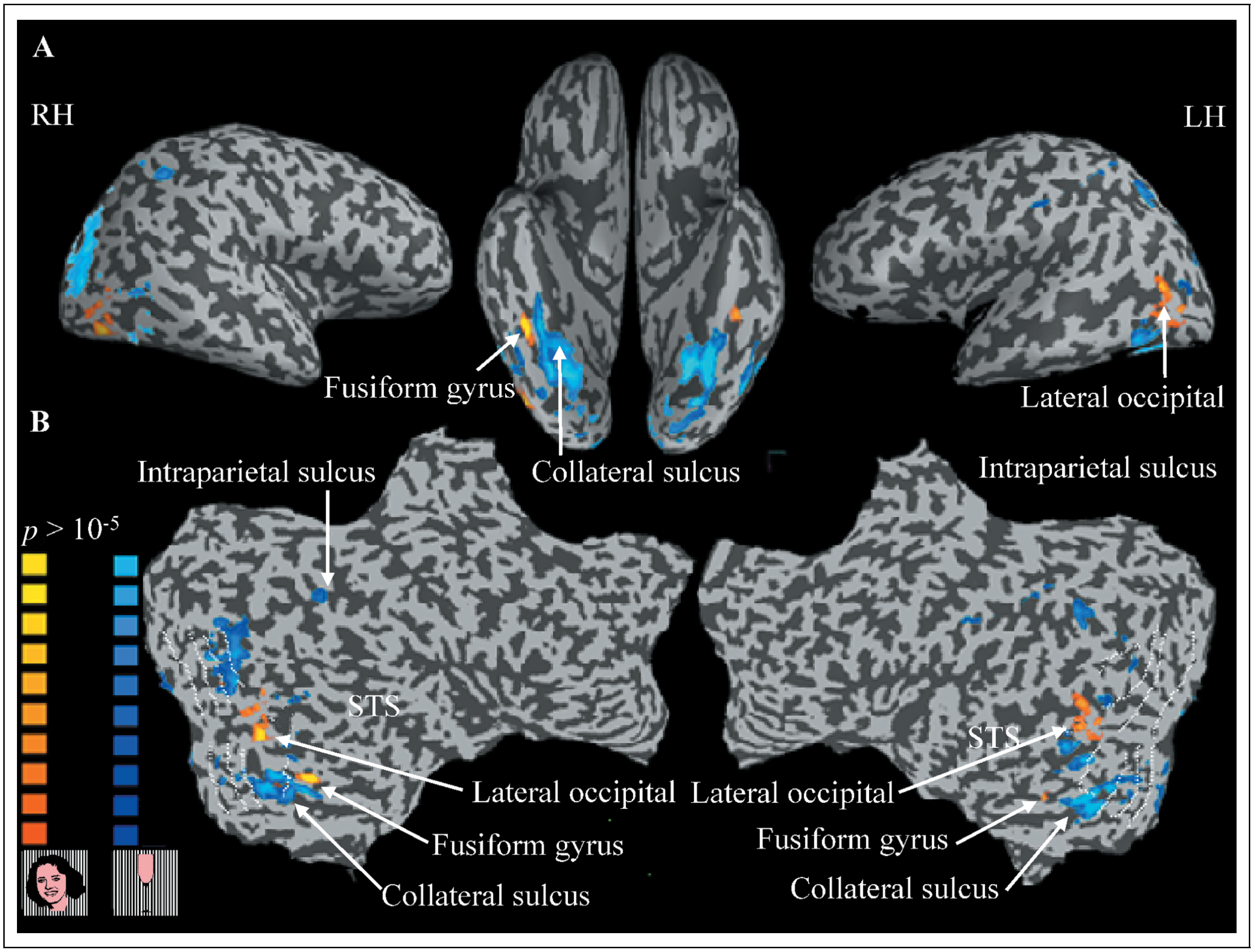

Figure 3. Object selectivity in the occipito-temporal cortex: (A) Lateral right, bottom and lateral left views of inflated brain present the face-related regions in the posterior fusiform gyrus and lateral occipital cortex (red) versus the control object (tumbler) activated regions (blue). The regions were highlighted according to their relative activation to the front face versus tumbler drawings. (B) The same data superimposed on the unfolded right and left hemispheres. Note the two localized face-related foci of activation.

signal for each condition can be seen in Figure 4B–D. Figure 4B shows the activation to the striped profiles and uniform vase conditions (Experiment 1) in the lateral occipital face-related region. As can be seen, significantly higher activation to the striped-profiles images compared to the uniform-vase images was found in this region ($p < .02$, two-tailed paired t test, $n = 6$), despite the presence of essentially identical local features in the two states. Preferential activation to striped profiles compared to uniform vases ($p < .01$, two-tailed paired t test, $n = 6$) was also seen in the posterior fusiform face-related region (Figure 4D, Experiment 1). Thus, holistic grouping effects were sufficient to significantly modulate the activation level in the occipito-temporal face-related regions.

In contrast to face-related voxels, which were easily localized using the preferential activation to front faces, we were unable to find a significant number of voxels that were preferentially activated to uniform vases compared to other objects or the front face images. This is due most likely to a relatively sparse representation of this type of objects in human high-order areas.

Could Other Factors Explain the Results?

It could be argued that the difference in the peripheral frame present in the "striped profiles" and "uniform vase" conditions could have been responsible for the differential activation pattern. In order to control for this possibility, we examined, in a separate experiment, the activation in the face-related regions to the uniform-profiles and the uniform-vase conditions. Note that the uniform-profiles and the uniform-vase conditions share the same peripheral striped frame. Note also that the uniform profiles and the striped profiles are markedly different in their local feature structure. The results of this experiment are shown in Figure 4B–D, Experiment 2. Despite the similarity in the peripheral frame, the face-selective regions were activated more by the uniform-profiles stimuli compared to the uniform-vase

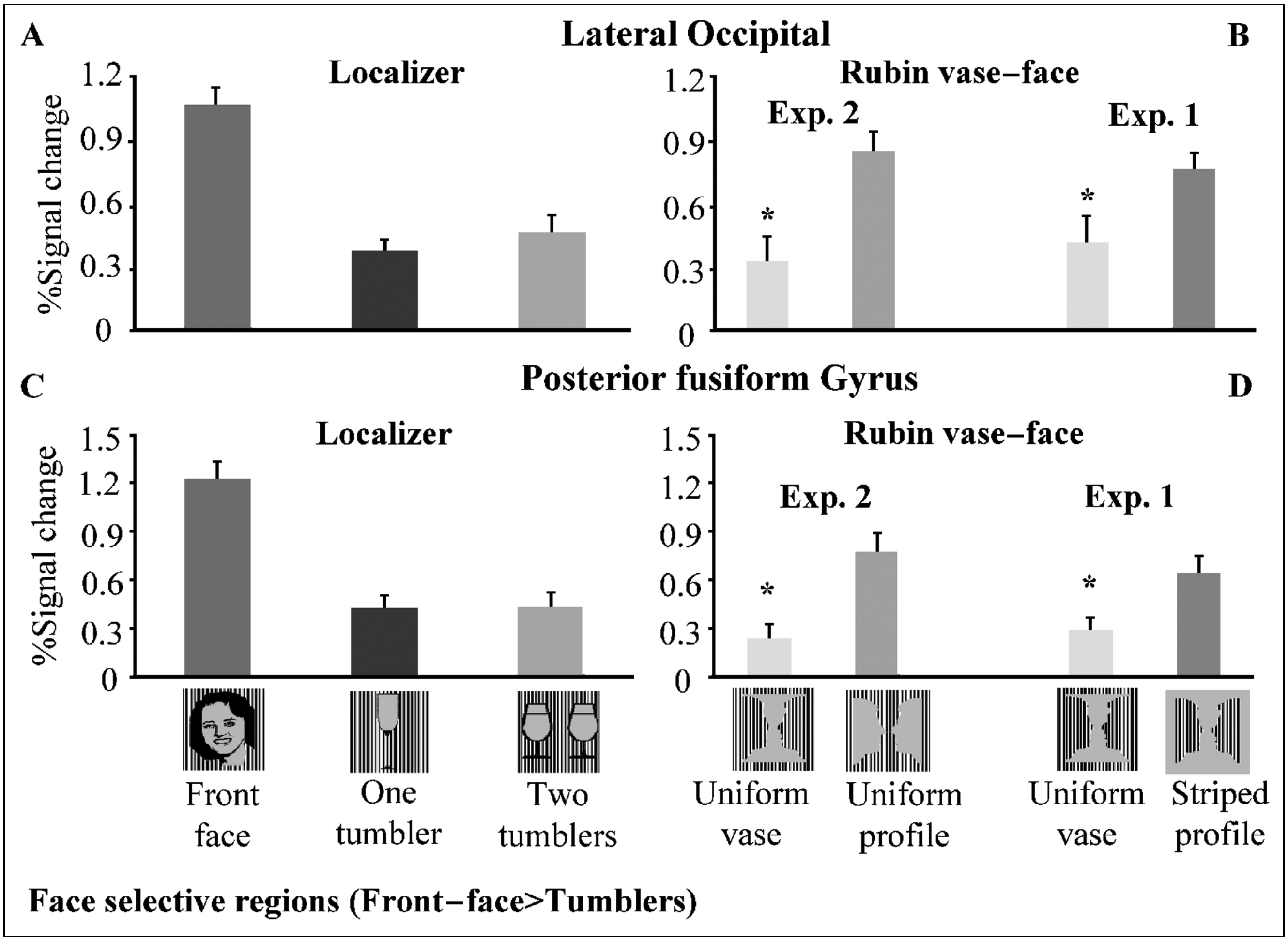

Figure 4. Activation profile in the face-related regions: The mean MR signal change for each condition in the lateral occipital face-related region (A, B), and the posterior fusiform face-related region (C, D). Signal change was obtained from voxels that showed preferential activation to front-face stimuli compared to the tumbler stimuli (localizer conditions, see Figure 3). The modified Rubin vase–face conditions were not included in the statistical test used to define the face-selective areas. Histograms on the left (A–C) show the mean MR signal for the localizer conditions averaged across the two experiments ($n = 16$). Histograms on the right (B–D) present the MR signal for the Rubin vase–face conditions in each experiment: uniform vase versus striped profiles (Experiment 1, $n = 6$) and uniform vase versus uniform profiles (Experiment 2, $n = 10$). Error bars indicate *SEM*. Asterisks denote significantly stronger activation ($p < .05$) elicited by stripe profiles or uniform profiles compared to uniform vase. Note that the face-related regions showed significantly higher activation to the striped profiles compared to the uniform vase condition, despite the presence of nearly identical local features in the two conditions.

stimuli. This effect occurred both in the fusiform gyrus ($p < .01$, two-tailed paired t test, $n = 10$), and in the lateral occipital region ($p < .01$, two-tailed paired t test, $n = 9$). Furthermore, despite the marked difference in the local feature structure, the two types of face profiles activated these regions to a similar degree (fusiform gyrus: $p < .63$, two-tailed t test, lateral occipital region: $p < .18$, two-tailed t test).

To exclude the possibility that the preferential activation to the profiles was due to attention shift to the two peripheral stimuli, we compared the activation in the face-related regions to the single central tumbler versus the two peripherally located tumblers (Figure 4A–C). No statistical differences between the central stimuli and the two peripheral stimuli were found in the fusiform gyrus ($p < .91$, two-tailed paired t test, $n = 16$), and the lateral occipital region ($p < .17$, two-tailed paired t test, $n = 16$).

To rule out the possibility that the activation differences were produced by gaze shifts to the peripheral stimuli, we measured eye movement in five subjects outside the magnet, using identical stimulus conditions. Throughout the eight and a half minutes of the experiment, gaze shifts were limited within a circle whose average diameter was 1.6 ± 0.44° (*SD*). On a few occasions (less than 16 times during the experiment), and without any correlation to a specific set of stimuli, subjects made a saccade outside this circle, but immediately returned to fixation. Furthermore, effects due to eye movements were minimized by the brief stimulus exposure (200 msec). Thus, we conclude that the modulation in activation when profiles were perceived was due to holistic grouping processes, and not to differences in stimulus features.

DISCUSSION

Using a modified version of the Rubin vase–face illusion we were able to dissociate between activation induced by local object features and activation induced by holistic, grouping processes that involve the entire object or large parts of it. Despite the resemblance in local features between the striped profiles and the uniform vase, there was a clear preferential response to profiles in face-related regions. The preferential activation could not be explained by the difference in the image outer frame since it was retained in the uniform-profile condition, which had a similar frame as the uniform-vase condition. Similarly, the differential activation could not be due to attention shift or eye gaze to peripheral stimuli since we did not find a similar preferential activation for two peripheral tumblers compared to a single central one. Thus, we conclude that holistic grouping processes contributed significantly to the selective activation in human face-related regions.

A series of neuroimaging studies have mapped cortical activity while dissociating the physical properties of the visual stimulus from the perceptual state. These studies can be conceptually divided into two categories. In one set of experiments, images, which were not perceived originally as objects, became recognizable following conditioning procedures (e.g., priming). For example, Dolan et al. (1997) have shown rapid positive priming effects for images that were originally difficult to recognize. Using a backward masking paradigm, Grill-Spector, Kushnir, Hendler, and Malach (2000) have shown a similar, albeit slow, positive priming effect. James, Humphrey, Gati, Menon, and Goodale (2000) have shown such priming effect for partially occluded objects. In another set of studies, identical visual images produced differential, category-specific activation depending on the perceptual state of the subject. Thus, O'Craven, Downing, and Kanwisher (1999) have demonstrated that attending to faces and houses in pictures that contain both images modulates activation in face-related and house-related regions, respectively. Differential activation was also obtained using a binocular rivalry setting, in which simultaneous presentation of different images to each eye results in perceptual alternation between the two images (Polonsky, Blake, Braun, & Heeger, 2000; Leopold & Logothetis, 1999; Tong, Nakayama, Vaughan, & Kanwisher, 1998). Tong et al. (1998) have shown that in face-related and house-related regions, fMRI activation is modulated during binocular rivalry according to the perceptual state of the observer.

All these studies provide an elegant illustration of the fact that the activation in high-order object areas is not solely dependent on the retinal image and can be modulated by high-order effects such as priming and attention. In that sense they are compatible with the findings presented here, which also show a departure of neuronal activation from strict dependence on the physical properties of the visual stimulus.

However, with regard to the specific question posed in the present study—is there a contribution of holistic processes to the preferential face-related activation of human cortex; these studies are not fully conclusive. The first set of studies is indeed strongly indicative of the operation of holistic processes that transcend the local feature structure; however, these studies pertain only to increases in image recognizability, and do not relate to perceptual transitions from one category to another. The second set of studies, on the other hand, involves category-specific effects, but can be explained by local feature activation rather than holistic processes. Thus, in the attention effects reported by O'Craven et al. (1999) the modulation in activity could conceivably be due to subject's attending to distinct local features specific to the house or face images. Similarly, in binocular rivalry, the transition between perceptual states could be produced by interocular competition between local features presented to each eye. Such competition can happen even at the level of V1. Indeed, activity modulation in human V1 has been recently demonstrated during binocular rivalry (Polonsky et al., 2000). To rule out the involvement of interocular competition will necessitate special experimental manipulations such as rapid interocular alteration of image presentation (Logothetis, Leopold, & Sheinberg, 1996).

The vase–face images used in the present study are unique in combining both holistic processing and category-specific modulation. On the one hand, unlike the first set of experiments, the vase–face modulation entails a transition from perceiving one object type (profile) to another (vase) rather than changing from a state of no recognition to recognition. On the other hand, unlike the second set of experiments, the vase–face transitions depend on closure effects, which are holistic by nature and cannot depend solely on local feature differences. Thus, our study provides strong evidence for the involvement of holistic processes in face-related regions of occipito-temporal cortex.

Several lines of research have suggested that face recognition is special, stressing the importance of holistic configuration of faces compared to other kinds of objects (Moscovitch & Moscovitch, 2000; Farah, Wilson, Drain, & Tanaka, 1998; Wang, Tanifuji, & Tanaka, 1998). Our results are compatible with a role for holistic processes in face representation, but it remains to be tested whether they are exclusive to faces or can be extended to other objects as well. The notion that holistic processes operate in the representation of other object categories received support in a recent report (Kourtzi & Kanwisher, 2000b). Using fMRI adaptation (Kourtzi & Kanwisher, 2000a; Grill-Spector et al., 1999) it was shown that the global shape of an object rather than its local feature structure affected the adaptation level. Together with our results, these findings point to holistic processes as a general property of high-level human object areas.

Other Relevant Studies

A different perceptual process inherent in bistable figures is the transition between states. Kleinschmidt, Buchel, Zeki, and Frackowiak (1998) found activation related to such transitions both in parietal and, interestingly, occipito-temporal cortex. The relationship between the transition-induced activation and the face-specific activation, found in our study, is unclear at present. Another study explored grouping effects in human V1 by comparing activation to motion, color, and luminance-defined checkerboards relative to control conditions containing only one of the two features of the checkerboards (Skiera, Petersen, Skalej, & Fahle, 2000). However, in this study it is not clear whether such activation reflects a truly holistic process or the influence of local cues induced by the combination of features.

Our findings are compatible with the possibility that global grouping processes may start at earlier stages such as areas V2 and V4. Several recent single-unit recording studies in monkeys found significant modulation of neuronal response as a function of the border ownership in V2 and V4, and to a lesser extent in V1 (Zhou et al., 2000; Lee et al., 1998; Zipser et al., 1996; Lamme, 1995). Recent fMRI studies found increased activation to illusory contours in V2 (Hirsch et al., 1995) and particularly at the lateral occipital complex (Mendola et al., 1999). The occipito-temporal cortex may play an essential role in long-range grouping operations by using its large bilateral receptive fields. However, at this stage, the nature of the segmentation mechanism operating in the occipito-temporal cortex and its relation to low-level grouping effects is still unclear.

A Role for Local Features

Our results do not exclude a contribution by local object features to face-related activation. The fact that the profile silhouettes activated these regions to a lesser extent compared to the more naturalistic and detailed image of the front-face line drawing (Figure 4), suggests that the level of activation in these regions increases also with the number, or complexity, of local visual features depicted in the image (Grill-Spector, Kushnir, Hendler, et al., 1998).

In conclusion, our finding of preferential activation for "face profiles" compared to "vase" images, despite their similar local feature structure, provides a clear unequivocal evidence that global grouping processes contribute to face-related activation in human occipito-temporal cortex.

MATERIALS AND METHODS

Subjects

Seventeen healthy volunteers (ages 26–49) participated in the experiments: 6 (3 women and 3 men) participated in the first experiment and 10 (5 women and 5 men) in the second. One subject was discarded due to problems in data acquisition. The Tel-Aviv Sourasky Medical Center Ethic Committee approved the experimental procedure.

Visual Stimuli

The stimuli subtended 15° × 15°. Contours of the Rubin profile were produced by tracing edges of face photographs. By duplicating each profile outline, a vase that shares the exact outline with the profiles was constructed. The stimuli were generated on a PC, and projected via an LCD projector onto a tangent screen located in the scanner.

Experimental Design

An interleaved-blocked presentation design was used in each experiment. Each scan consisted of 32 stimulus epochs. In the first experiment, pictures of faces, striped profiles, and colored uniform vases were presented in 8 blocks of 9 sec each. Pictures of 1 tumbler and 2 tumblers were presented in 4 blocks of 9 sec each. The same design was used in the second experiment, exchanging pictures of striped profiles with pictures of colored uniform profiles. Each 9-sec epoch was followed by a 6-sec blank. Nine different images of the same type were presented in each epoch. During the experiment, subjects were instructed to decide whether they saw two identical pictures in a row or not (one-back memory task). One or two consecutive repetitions of the same image occurred in each epoch. This one-back matching task was used to engage the viewer in the perceptual task.

MRI Acquisition

The BOLD fMRI measurements were performed in a whole-body 1.5-T GE scanner. A custom quadrature surface coil (Nova Medical, Wakefield, MA) was used to provide a high signal-to-noise ratio in occipito-temporal brain regions. Functional images were acquired using a susceptibility-sensitive EPI pulse sequence (T2*, TR = 3 sec, TE = 55 msec, flip angle = 90°, imaging matrix = 80 × 80, FOV = 24 cm). Data were collected from 17 horizontal, 4-mm–thick slices, with 1-mm gap between slices.

Data Analysis

The data were reconstructed and analyzed with the "Brain-voyager 4.01" software package (Brain Innovation, Maastricht, Netherlands). The original 17 2-D EPI slices of each subject were aligned with a 3-D anatomical volume scan (T1 SPGR sequence) and converted to Talairach coordinates. Prior to statistical analysis, a 3-D motion correction algorithm and a temporal band-pass filter was applied to the data. A general linear model (GLM) analysis was applied on each voxel. Only voxels at the significant level of $p < 10^{-5}$ (uncorrected) were included in the statistical map. Clusters of 6 or more contiguous voxels were considered significant. The obtained activation maps were superimposed on an inflated and unfolded cortex for each subject. Talairach coordinates were determined for the centers of each ROI.

Eye Movement

Eye movements were monitored outside the scanner, using identical visual stimuli and task, using video-base eye tracker (EyeLink SR-Research, Toronto, Canada), to ensure that there were no differential patterns of eye movements across the central and peripheral stimuli.

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The data reported in this experiment have been deposited in the National fMRI Data Center (http://www.fmridc.org). The accession number is 2-2001-IIIP8.

REFERENCES

Aguirre, G. K., Zarahn, E., & D'Esposito, M. (1998). An area within human ventral cortex sensitive to "building" stimuli: Evidence and implications. *Neuron, 21,* 373–383.

Dolan, R. J., Fink, G. R., Rolls, E., Booth, M., Holmes, A., Frackowiak, R. S., & Friston, K. J. (1997). How the brain learns to see objects and faces in an impoverished context. *Nature, 389,* 596–599.

Epstein, R., & Kanwisher, N. (1998). A cortical representation of the local visual environment. *Nature, 392,* 598–601.

Farah, M. J., Wilson, K. D., Drain, M., & Tanaka, J. N. (1998). What is "special" about face perception? *Psychological Review, 105,* 482–498.

Gilaie Dotan, S., Ullman, S., Kushnir, T., Steinberg, I., & Malach, R. (2000). Stereo Gestalt effects in human object related visual areas. *Society for Neuroscience Abstracts, 26,* 1333.

Grill-Spector, K., Kushnir, T., Edelman, S., Itzchak, Y., & Malach, R. (1998). Cue-invariant activation in object-related areas of the human occipital lobe. *Neuron, 21,* 191–202.

Grill-Spector, K., Kushnir, T., Hendler, T., Edelman, S., Itzchak, Y., & Malach, R. (1998). A sequence of object-processing stages revealed by fMRI in the human occipital lobe. *Human Brain Mapping, 6,* 316–328.

Grill-Spector, K., Kushnir, T., Edelman, S., Avidan, G., Itzchak, Y., & Malach, R. (1999). Differential processing of objects under various viewing conditions in the human lateral occipital complex. *Neuron, 24,* 187–203.

Grill-Spector, K., Kushnir, T., Hendler, T., & Malach, R. (2000). The dynamics of object-selective activation correlate with recognition performance in humans. *Nature Neuroscience, 3,* 837–843.

Halgren, E., Dale, A. M., Sereno, M. I., Tootell, R. B. H., Marinkovic, K., & Rosen, B. R. (1999). Location of human face-selective cortex with respect to retinotopic areas. *Human Brain Mapping, 7,* 29–37.

Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences, 4,* 223–233.

Hirsch, J., DeLaPaz, R. L., Relkin, N. R., Victor, J., Kim, K., Li, T., Borden, P., Rubin, N., & Shapley, R. (1995). Illusory contours activate specific regions in human visual cortex: Evidence from functional magnetic resonance imaging. *Proceedings of the National Academy of Sciences, U.S.A., 92,* 6469–6473.

Ishai, A., Ungerleider, L. G., Martin, A., Schouten, H. L., & Haxby, J. V. (1999). Distributed representation of objects in the human ventral visual pathway. *Proceedings of the National Academy of Sciences, U.S.A., 96,* 9379–9384.

James, T. W., Humphrey, G. K., Gati, J. S., Menon, R. S., & Goodale, M. A. (2000). The effects of visual object priming on brain activation before and after recognition. *Current Biology, 10,* 1017–1024.

Kanwisher, N., Chun, M. M., McDermott, J., & Ledden, P. J. (1996). Functional imagining of human visual recognition. *Cognitive Brain Research, 5,* 55–67.

Kleinschmidt, A., Buchel, C., Zeki, S., & Frackowiak, R. S. (1998). Human brain activity during spontaneously reversing perception of ambiguous figures. *Proceedings of the Royal Society of London, Series B: Biological Sciences, 265,* 2427–2433.

Kourtzi, Z., & Kanwisher, N. (2000a). Cortical regions involved in perceiving object shape. *Journal of Neuroscience, 20,* 3310–3318.

Kourtzi, Z., & Kanwisher, N. (2000b). Processing of object structure versus contours in the human lateral occipital cortex. *Society for Neuroscience Abstracts, 26,* 1332.

Lamme, V. A. (1995). The neurophysiology of figure–ground segregation in primary visual cortex. *Journal of Neuroscience, 15,* 1605–1615.

Lee, T. S., Mumford, D., Romero, R., & Lamme, V. A. (1998). The role of the primary visual cortex in higher level vision. *Vision Research, 38,* 2429–2454.

Leopold, D. A., & Logothetis, N. K. (1999). Multistable phenomena: Changing views in perception. *Trends in Cognitive Sciences, 3,* 254–264.

Logothetis, N. K., Leopold, D. A., & Sheinberg, D. L. (1996). What is rivalling during binocular rivalry? *Nature, 380,* 621–624.

Malach, R., Reppas, J. B., Benson, R. R., Kwong, K. K., Jiang, H., Kennedy, W. A., Ledden, P. J., Brady, T. J., Rosen, B. R., & Tootell, R. B. (1995). Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proceedings of the National Academy of Sciences, U.S.A., 92,* 8135–8139.

Mendola, J. D., Dale, A. M., Fischl, B., Liu, A. K., & Tootell, R. B. (1999). The representation of illusory and real contours in human cortical visual areas revealed by functional magnetic resonance imaging. *Journal of Neuroscience, 19,* 8560–8572.

Moscovitch, M., & Moscovitch, D. A. (2000). Super face-inversion effects for isolated internal or external features, and for fractured faces. *Cognitive Neuropsychology, 17,* 201–219.

O'Craven, K. M., Downing, P. E., & Kanwisher, N. (1999). fMRI evidence for objects as the units of attentional selection. *Nature, 401,* 584–587.

Polonsky, A., Blake, R., Braun, J., & Heeger, D. J. (2000). Neuronal activity in human primary visual cortex correlates with perception during binocular rivalry. *Nature Neuroscience, 3,* 1153–1159.

Skiera, G., Petersen, D., Skalej, M., & Fahle, M. (2000). Correlates of figure–ground segregation in fMRI. *Vision Research, 40,* 2047–2056.

Tanaka, K. (1996). Inferotemporal cortex and object vision. *Annual Review of Neuroscience, 19,* 109–139.

Tanaka, K., Saito, H., Fukada, Y., & Moriya, M. (1991). Coding visual images of objects in the inferotemporal cortex of the macaque monkey. *Journal of Neurophysiology, 66,* 170–189.

Tong, F., Nakayama, K., Vaughan, J. T., & Kanwisher, N. (1998). Binocular rivalry and visual awareness in human extrastriate cortex. *Neuron, 21,* 753–759.

Tong, F., Nakayama, K., Moscovitch, M., Weinrib, O., & Kanwisher, N. (2000). Response properties of the human fusiform face area. *Cognitive Neuropsychology, 17,* 257–279.

Wang, G., Tanifuji, M., & Tanaka, K. (1998). Functional architecture in monkey inferotemporal cortex revealed by in vivo optical imaging. *Neurosciences Research, 32,* 33–46.

Zhou, H., Friedman, H. S., & von Der Heydt, R. (2000). Coding of border ownership in monkey visual cortex. *Journal of Neuroscience, 20,* 6594–6611.

Zipser, K., Lamme, V. A., & Schiller, P. H. (1996). Contextual modulation in primary visual cortex. *Journal of Neuroscience, 16,* 7376–7389.