

Texture Segregation in the Human Visual Cortex: A Functional MRI Study

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Kastner, Sabine, Peter De Weerd, and Leslie G. Ungerleider. Texture segregation in the human visual cortex: a functional MRI study. *J. Neurophysiol.* 83: 2453–2457, 2000. The segregation of visual scenes based on contour information is a fundamental process of early vision. Contours can be defined by simple cues, such as luminance, as well as by more complex cues, such as texture. Single-cell recording studies in monkeys suggest that the neural processing of complex contours starts as early as primary visual cortex. Additionally, lesion studies in monkeys indicate an important contribution of higher order areas to these processes. Using functional MRI, we have investigated the level at which neural correlates of texture segregation can be found in the human visual cortex. Activity evoked by line textures, with and without texture-defined boundaries, was compared in five healthy subjects. Areas V1, V2/VP, V4, TEO, and V3A were activated by both kinds of line textures as compared with blank presentations. Textures with boundaries forming a checkerboard pattern, relative to uniform textures, evoked significantly more activity in areas V4, TEO, less reliably in V3A, but not in V1 or V2/VP. These results provide evidence that higher order areas with large receptive fields play an important role in the segregation of visual scenes based on texture-defined boundaries.

INTRODUCTION

The segregation of visual scenes based on contour information is a fundamental process of early vision. In natural scenes, contour boundaries are mainly extracted on the basis of simple cues, such as luminance, color, or motion, but they can also be defined by more complex cues, such as texture or illusory contours.

Single-cell recording studies have shed light on the mechanisms underlying complex contour perception. Responses to oriented bars presented within a neuron's receptive field (RF) and surrounded by an array of bars at the same or orthogonal orientation outside the RF were studied in V1 of anesthetized and awake animals (Kastner et al. 1997, 1999b; Knierim and Van Essen 1991; Nothdurft et al. 1999). Neurons responded more strongly to the bar inside the RF when it was surrounded by orthogonal bars, that is, when it was perceptually salient, "popping out" from the texture background. Similarly, neurons in V1 showed stronger responses to texture elements belonging to a figure defined by texture boundaries than to elements belonging to a background (Lamme 1995; Zipser et al. 1996). Neurons in V1 and V2 have also been found to respond to other

complex contours, such as illusory boundaries (Grosf et al. 1993; Sheth et al. 1996; Von der Heydt and Peterhans 1989). These findings suggest that the segregation of visual scenes based on complex contour information starts at early stages of cortical processing.

It remains unclear, however, how neurons in V1 and V2 integrate information from regions beyond their RFs. One possibility is that neural responses to complex contours are generated within early visual areas via intrinsic long-range horizontal connections (Das and Gilbert 1999). Another possibility is that these responses are mediated via feedback projections from higher order visual areas that integrate information from more extensive portions of the visual field by virtue of their large RFs. Results from lesion studies support the latter view. Monkeys with ablations of area V4 and cats with extensive extrastriate lesions are impaired in the perception of illusory or texture-defined contours (DeWeerd et al. 1993, 1994, 1996; Merigan 1996), suggesting that higher order areas play an important role in the perception of complex contours.

In humans, recent functional brain-imaging studies have demonstrated that the perception of illusory contours, motion-defined contours, or structure from motion is associated with activations in several extrastriate visual areas (ffytche and Zeki 1996; Grill-Spector et al. 1998; Hirsch et al. 1995; Mendola et al. 1999; Reppas et al. 1997; Tyler and Baseler 1998; Van Oostende et al. 1997). However, little is known about the areas activated by static texture-defined contours, as typically used in single-unit and visually evoked potential studies (e.g., Bach and Meigen 1992; Lamme et al. 1992). The goal of the present study was therefore to investigate at which level neural correlates of texture segregation can be found in the human visual cortex. Activations evoked by line textures, which have been shown to activate ventral occipitotemporal areas (Beason-Held et al. 1998; Gulyas et al. 1998; Puce et al. 1996), were studied when presented as uniform textures compared with segregated textures containing boundaries that formed a checkerboard pattern. Part of this work has been published in abstract form (De Weerd et al. 1998).

METHODS

Five subjects (3 females, aged: 22–35) gave their informed written consent to participate in the study, which was approved by the NIMH Institutional Review Board. A more detailed description of scanning procedures, image processing, statistical procedures, and retinotopic mapping is given in Kastner et al. (1998, 1999a).

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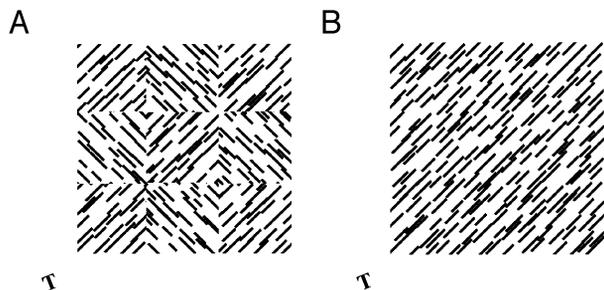


FIG. 1. Visual stimuli. Line textures (8×8 deg in size, centered at 8 deg eccentricity) were presented to the right upper quadrant while subjects fixated. One texture was uniform (A), the other a checkerboard defined by texture boundaries (B). The uniform texture contained line elements (0.4×0.05 deg) at identical orientation alternating at 1 Hz between 45 and 135 deg. The boundaries of the checkerboard texture were defined by the orientation difference between line elements at 45 and 135 deg alternating at 1 Hz. In the actual experiment, bright lines were presented on a dark background. Textures were presented in blocks of 18 s interleaved with blank periods.

Visual task

Line textures, 8×8 deg in size, were presented to the upper right quadrant centered at 8 deg eccentricity from a fixation point (element size: 0.4×0.05 deg with length and width randomization of 30%; element spacing of 0.3 deg with spacing randomization of 40%). Textures were presented in two different conditions: uniform (UT) or segregated (ST) (Fig. 1). The uniform textures contained line elements of identical orientation alternating at 1 Hz between 45 and 135 deg. The segregated textures consisted of nine squares (2.66×2.66 deg each) forming a checkerboard pattern. The boundaries of each square were defined by the orientation contrast between line elements at 45 and 135 deg alternating at 1 Hz. The density of the line elements within each square was kept constant, resulting in an equal distribution of mean luminance across the pattern. A 2D Fourier analysis was performed to confirm the lack of Fourier components along the texture boundaries. Visual stimuli were presented to the subjects as videotapes rear-projected onto a translucent screen placed 40 cm from the subjects' feet. Stimuli were viewed from inside the bore of the magnet via a mirror system attached to the head coil. During a given scan, uniform and segregated textures were presented in alternating blocks of 18 s each interleaved with blank periods. Each scan started with a blank period of 36 s and ended with a blank period of 18 s. The subjects' task was to maintain fixation at a central fixation point and to count the letters T or L, presented there for 250 ms in random order at 4 Hz. The T/L task had a high attentional load to ensure proper fixation and to prevent subjects from covertly attending to the peripheral stimuli (Kastner et al. 1998). When debriefed after the experiment, subjects reported that they were not aware of any differences between the texture stimuli.

Data acquisition and analysis

Fourteen contiguous, coronal, 5-mm-thick slices were acquired in 12 series of 60 images each, starting from the posterior pole (in-plane resolution 2.5×2.5 mm). Gradient echo, echo planar imaging was used (TR = 3 s, TE = 40 ms, flip angle = 90 deg) on a 1.5 Tesla GE magnet using a standard head coil. Functional images were coaligned with a high-resolution anatomic scan taken in the same session (3D SPGR, TR = 15 ms, TE = 7 ms, flip angle = 30 deg, 256×256 matrix, FOV = 160×160 mm, 28 coronal slices, thickness: 5 mm).

Images were motion-corrected (Woods et al. 1993), spatially smoothed in-plane with a small Gaussian filter (FWHM of 1.2 voxel lengths), and ratio-normalized to the same global mean intensity (Friston et al. 1991). Statistical analyses were performed on both smoothed and unsmoothed data. Activations were identified by means of multiple regression analysis of the time series of MRI intensities in

every voxel and two regressors of interest (Friston et al. 1995), reflecting contrasts between 1) both texture presentations versus blank periods and 2) segregated texture versus uniform texture presentations. Additional regressors were used to factor out variance due to between-run changes in mean intensity and within-run linear changes. The statistical significance ($P < 0.05$) of activated regions was assessed by an analysis based on the spatial extent of each region (Friston et al. 1994; Poline et al. 1997). Activated voxels were assigned to areas V1, V2, and VP, as identified on the basis of retinotopic mapping of the horizontal and vertical meridians, and to areas V4, TEO, and V3A on the basis of upper (UVF) and lower visual field (LVF) topography, performed on all subjects in a separate scan session. High color- and luminance-contrast checkerboard stimuli extending over the central 10–12 deg were presented along the meridia. The UVF and LVF representations are separated in V4 and located medially and laterally, respectively, on the fusiform gyrus in ventral occipitotemporal cortex, whereas this separation is not seen in the region anterior to V4, which we term TEO. Area V4 in this study likely corresponds to area V4 of McKeefry and Zeki (1997) and appears to overlap with V4v and V8 described by Hadjikhani et al. (1998). Unlike V4 and TEO, V3A is located dorsally in occipital cortex, where the UVF and LVF are represented (Tootell et al. 1997). The fMRI time series, averaged over all activated voxels in a given region during texture presentations versus blank presentations (thresholded at a Z score of 2.3) and over runs for each subject, are presented as group data. Statistical significance was assessed with repeated measures of analysis of variance (ANOVAs) on the six peak intensities of the fMRI signal during a given presentation block. Differences in responses (R) to the different texture conditions were quantified by a texture segregation index [$TSI = (R_{ST} - R_{UT}) / (R_{ST} + R_{UT})$]. For each subject, statistical maps and structural images were transformed into Talairach space (Talairach and Tournoux 1988) by using the template from SPM96b to obtain normalized coordinates of the activations.

RESULTS

Segregated and uniform line textures as compared with blank presentations evoked significant activity in visual areas V1, V2, VP, V4, and V3A of the left hemisphere in all subjects, and in TEO of the left hemisphere in four of five subjects. With the exception of V3A, the locations of the activations were in the ventral parts of these areas, consistent with the presentation of texture stimuli to the upper right visual field. For area V3A, the activations were located dorsally in the left hemisphere. This is illustrated for a single subject in Fig. 2A. As the border between V2 and VP could not be distinguished unequivocally in some of the subjects, the combined region will henceforth be referred to as V2/VP. Mean Talairach coordinates (and activated volumes), averaged across all subjects, were as follows: V1 ($1,000 \text{ mm}^3$): $x = -2.5, y = -84, z = +10$; V2/VP ($1,328 \text{ mm}^3$): $-4, -83, -8$; V4 ($2,273 \text{ mm}^3$): $-17, -76, -17$; TEO ($1,760 \text{ mm}^3$): $-23, -57, -13$; V3A (813 mm^3): $-22, -88, +24$. For the subject shown in Fig. 2, the texture segregation patterns evoked significantly more activity than the uniform texture patterns in areas V2/VP and V4 (Fig. 2B). Stronger activation of V4 by segregated textures than by uniform textures was found in all subjects. Such response differences were also seen in other visual areas in individual subjects, but less consistently.

An analysis of the time series of the fMRI signal (Fig. 3) and the mean signal changes (Fig. 4A) averaged across subjects revealed that segregated textures evoked stronger responses in V4 ($P < 0.01$), TEO ($P < 0.05$), and V3A ($P < 0.05$) with

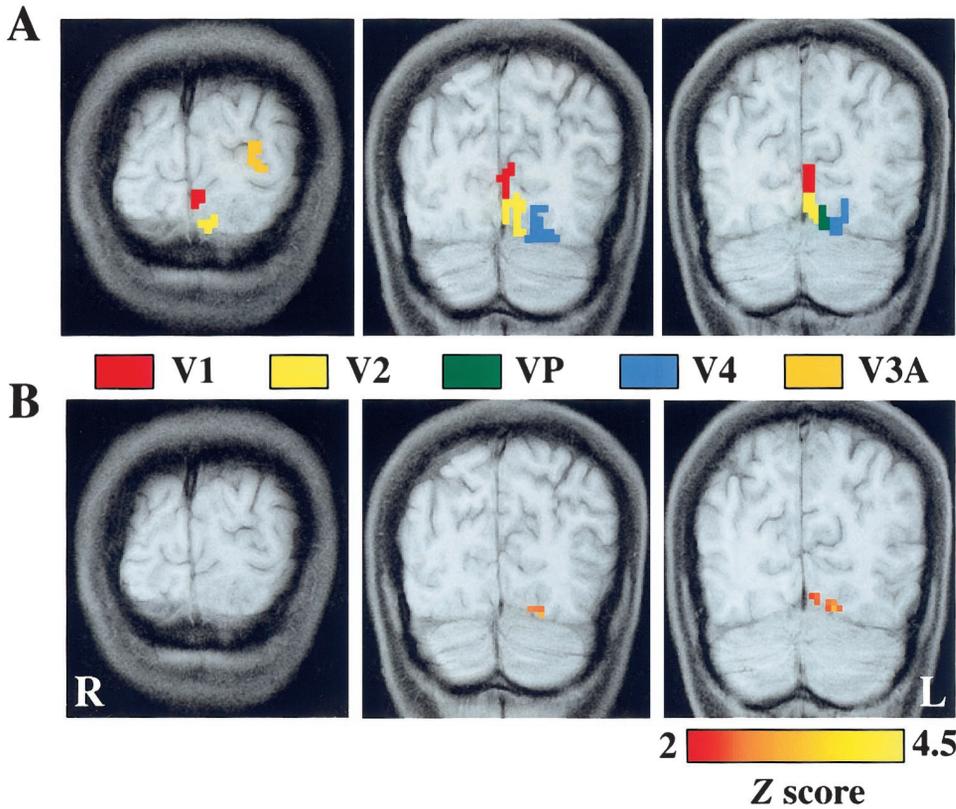


FIG. 2. Activated regions in the human visual cortex. *A*: brain areas activated by uniform and segregated textures compared with blank presentations. Coronal slices of a single subject at $y = -90, -80,$ and -75 mm, respectively. Activated voxels were assigned to areas V1, V2, VP, V4, and V3A as determined by meridian mapping and upper (UVF) and lower (LVF) visual field topography. In each coronal plane, representations of vertical and horizontal meridians extending over the central 12 deg were determined by presenting high color- and luminance-contrast checkered stimuli along the meridians flickering at 4 Hz. For UVF and LVF topography, complex colorful stimuli were presented to the upper or lower visual field. The UVF and LVF are separated in V4 and located medially and laterally, respectively, on the fusiform gyrus, whereas this separation is not seen in the region anterior to V4, termed TEO. *B*: brain areas activated more strongly by segregated textures than by uniform textures. Same subject and slices as in *A*. Segregated textures evoked significantly more activity than uniform textures in V2/VP and V4.

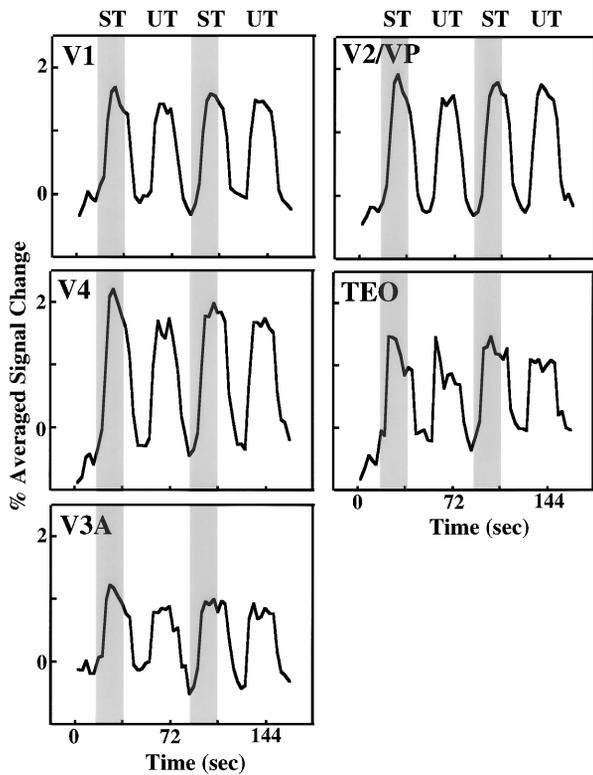


FIG. 3. Time series of functional MRI signals in V1, V2/VP, V4, TEO, and V3A averaged across subjects. Segregated textures evoked significantly more activity than uniform textures in V4, TEO, and V3A, but not in V1 or V2/VP. ST, blocked presentations of segregated textures. UT, blocked presentations of uniform textures.

response differences on the order of about 0.3%. In V1, the differences in responses to the two texture conditions were not significant. In V2/VP, there was a trend toward stronger responses to segregated textures ($P = 0.08$). The interaction between area and texture condition was significant ($P < 0.01$). These results are also reflected in the texture segregation index (Fig. 4*B*). The first presentation block (i.e., the segregated textures) evoked a stronger transient response in most of the areas than subsequent texture presentations, but the differences in responses to segregated and uniform texture were not due to this transient onset signal. First, the difference between the first and the second presentation of the segregated textures (block 1 and 3 in Fig. 3) was not significant in any visual area, and

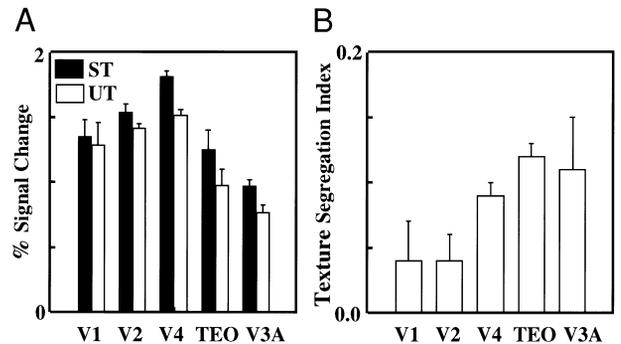


FIG. 4. Mean signal changes and texture segregation index (TSI). *A*: percent signal changes in V1, V2/VP, V4, TEO, and V3A, averaged across subjects. Bars labeled V2 refer to V2/VP. For each subject, six peak intensities of the fMRI signal obtained during ST and UT presentations were averaged. *B*: TSI increased from early areas V1 and V2/VP to higher order areas V4, TEO, and V3A, indicating increasing differences in response to segregated and uniform textures. Bars, mean \pm SE.

second, the response differences between the second presentations of segregated and uniform textures (block 3 and 4 in Fig. 3) were significant in V4 ($P < 0.01$) and TEO ($P < 0.05$). In V3A, the latter analysis did not reach significance ($P = 0.08$), so that the contribution of transient onset signals to the effect in this area cannot be excluded. These findings suggest an important role of higher order areas V4, TEO, and probably V3A in processing texture-defined boundaries.

DISCUSSION

The present study investigated the level at which texture-defined contours are being processed in the human visual cortex. Neural correlates of texture segregation were identified in higher order areas V4, TEO, and less consistently, V3A, which were more strongly activated by segregated textures than by uniform textures. The processing of complex contours defined by illusory boundaries has been explored in recent functional imaging studies (ffytche and Zeki 1996; Hirsch et al. 1995; Mendola et al. 1999). Activations in areas V3A, V4/V8, and V7 (an area just anterior to V3A) were shown to be associated with the processing of illusory contours (e.g., a Kanizsa square). We found that similar areas are involved in the processing of texture-defined contours. Further, our results suggest a gradual increase in the responsiveness of visual areas to texture-defined contours as one proceeds through the cortical hierarchy. Such a gradual increase in responsiveness to illusory contours has been shown most clearly by Mendola et al. (1999). These findings indicate that a common set of visual areas rather than a single one is involved in the perception of complex contours defined by texture or illusory boundaries in the human visual cortex.

The demonstration of an involvement of V4, TEO, and V3A in texture segregation underlines the important role of higher order areas in scene segmentation, as suggested by lesion studies in monkeys. Monkeys with ablations of area V4 show deficits in the perception of both texture-defined and illusory contours, but not of contours that are defined by simple cues, such as motion, color, or luminance (DeWeerd et al. 1996; Merigan 1996). From these findings, it may be concluded that higher order areas extract complex contour information, presumably by virtue of their large receptive fields, and modulate the responses of lower order areas to complex contours via feedback inputs. This idea is supported by recent findings that cortical feedback modulates both excitatory and suppressive inputs to neurons in lower-order areas (Hupe et al. 1998).

Single-cell recording studies in monkeys have identified neural correlates of texture-defined boundaries at the level of V1. Neural responses were shown to depend on the perceptual context in which visual stimuli were presented. For example, neurons responded more strongly to an oriented line when it was part of a "pop-out" texture than when it was part of a uniform texture (Kastner et al. 1997, 1999b; Knierim and Van Essen 1991; Nothdurft 1999), or they responded more strongly to texture elements when they were part of a texture segment standing out against a background than when they were part of the background (Lamme 1995; Zipser et al. 1996). Using fMRI, we failed to identify neural correlates of texture segregation in V1. It may be argued that this negative finding is due to the fact that the texture patterns were presented to the periphery and subjects were involved in a high attentional load

task at fixation, so that they did not perceive the segregation effect. However, neural correlates of pop-out and texture segregation have been identified in anesthetized animals (Kastner et al. 1999b; Nothdurft et al. 1992, 1999; but see Lamme et al. 1998). A second possibility is that the texture patterns used in the present study did not effectively activate V1 neurons, because the patterns were comprised of many texture-defined contours rather than consisting of a single figure standing out from a background. Further single-cell recording studies are needed to rule out this possibility. A third possibility is that the dimensions of our display favored more anterior extrastriate areas with larger RFs. However, several single-unit studies have shown that texture boundary effects occur over large spatial scales up to 10–12 deg in V1 (e.g., Knierim and Van Essen 1991; Lamme 1995). Hence, neurons in V1 should be well suited to detect texture boundaries that were separated, at the most, by 2.7 deg in our experiments. Finally, it may be that fMRI at 1.5 T is not sensitive enough to obtain signals related to texture segregation in V1. Future investigations using magnets at higher field strength will be needed to clarify this issue.

The present findings and those from single-cell physiology in anesthetized animals suggest that complex contour information can be processed outside the focus of attention. This view is further supported by studies in patients suffering from visual hemineglect. For example, Mattingley et al. (1997) reported a patient whose extinction was less severe when bilateral stimuli were arranged to form an illusory Kanizsa-square, demonstrating that the patient used the complex contour information from his neglected hemifield to form the percept of a common surface. Thus the findings from single-cell physiology, patients with attentional deficits, and functional brain-imaging converge to support the view that visual scene segmentation based on complex contour information requires little or no attentional resources (Braun and Sagi 1990; Treisman 1985).

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