The specificity of cortical region KO to depth structure

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Functional MRI studies have identified a cortical region designated as KO between retinotopic areas V3A/B and motion area V5 in human cortex as particularly responsive to motion-defined or kinetic borders. To determine the response of the KO region to more general aspects of structure, we used stereoscopic depth borders and disparate planes with no borders, together with three stimulus types that evoked no depth percept: luminance borders, line contours and illusory phase borders. Responses to these stimuli in the KO region were compared with the responses in retinotopically defined areas that have been variously associated with disparity processing in neurophysiological and fMRI studies. The strongest responses in the KO region were to stimuli evoking perceived depth structure from either disparity or motion cues, but it showed negligible responses either to luminance-based contour stimuli or to edgeless disparity stimuli. We conclude that the region designated as KO is best regarded as a primary center for the generic representation of depth structure rather than any kind of contour specificity.
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Introduction

The medial surface of occipital cortex is now well-established as being devoted to the primary visual projection areas V1–3 (Schneider et al., 1993; Engel et al., 1994; Sereno et al., 1995; DeYoe et al., 1996; Tootell et al., 1996; Engel et al., 1997; Hadjikhani et al., 1998; Smith et al., 1998). Consequently, efforts are switching to the analysis of lateral occipital cortex, which is much less strongly retinotopic. Functional MRI studies have identified a cortical area between retinotopic area V3A and motion area V5 in human cortex as particularly responsive to motion-defined borders, designated as the "kinetic occipital" region, KO (Van Oostende et al., 1997; Dupont et al., 1997; Grossman et al., 2000; Kononen et al., 2003). The typical location of this area relative to other activation sites on the lateral occipital cortex is shown in Fig. 1 (see Materials and methods).

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Zeki et al. (2003) have questioned the designation of this region as particularly responsive to kinetic borders, finding responses in the same cortical region to static forms presented via color grating borders described as equiluminant with no kinetic component. Indeed, Van Oostende et al. (1997) also reported significant responses in their KO region to stimuli with only luminance borders. Moreover, the chromatic segmentation stimuli used by Zeki et al. (2003) is a type often classed as containing subjective contours. Since the KO region lies within the lateral occipital area shown by Mendola et al. (1999) to respond well to subjective contours of the conventional kind (Kanizsa, 1978), one hypothesis is that the KO region is specialized for the processing of subjective contours in general rather than solely those that are defined kinetically.

A second property in common between the kinetic stimuli and the figure-ground stimuli of Zeki et al. (2003) is that they may both elicit depth segregation. The depth aspect of the stimuli is unremarked by all authors, but it is a strong perceptual component of their visual processing. If the depth structure of the stimuli is the key feature for the activation of the KO region, it raises the prediction that the KO region should be strongly responsive to depth structure generated by binocular disparity cues, in the absence of motion, luminance or subjective contours. Note that this hypothesis focuses on the activity underlying the perceptual experience of depth structure rather than the activation of disparity-specific neurons per se. These two types of neural activity (for disparity and for depth structure) may well be separate aspects of the full circuit for depth processing (Tyler, 1983, 1991; Tyler and Kontsevich, 1995).

At first sight, the depth structure hypothesis for activation of the KO region seems incompatible with the consensus result from previous neuroimaging studies in human, that V3A is the region of strongest response for stereoscopic stimuli (Ptito et al., 1993; Gulyas and Roland, 1994; Mendola et al., 1999; Kwee et al., 1999; Backus et al., 2001; Merboldt et al., 2002; Negawa et al., 2002; Gillaie-Dotan et al., 2002; Fortin et al., 2002). However, these studies need to be considered with care because in many of them V3A was defined purely by gyral landmarks that could have included more anterior regions, while those that use retinotopic criteria for V3A ignore activation in neighboring regions such as that corresponding to area KO.

Studies focusing on stereoscopic depth structure, such as Gulyas and Roland (1994), Mendola et al. (1999) and Tsao et al. (2003), report activation in lateral occipital regions that overlap
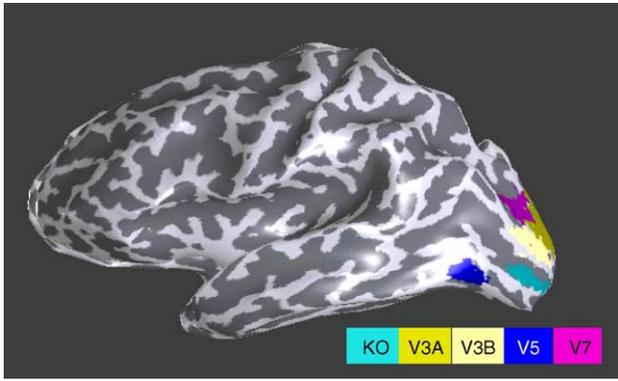
Fig. 1. Inflated reconstruction of segmented cortex of the left hemisphere of one observer, showing the locations of areas KO, V3A, V3B, V5 (hMT+) and V7 (see Materials and methods). Zeki et al. (2003) have questioned the designation of this region as particularly responsive to kinetic borders, finding responses in the same cortical region to static forms presented via color grating borders described as equiluminant with no kinetic component. Indeed, Van Oostende et al. (1997) also reported significant responses in their KO region to stimuli with only luminance borders. Moreover, the chromatic segmentation stimuli used by Zeki et al. (2003) is a type often classed as containing subjective contours. Since the KO region lies within the lateral occipital area shown by Mendola et al. (1999) to respond well to subjective contours of the conventional kind (Kanizsa, 1978), one hypothesis is that the KO region is specialized for the processing of subjective contours in general rather than solely those that are defined kinetically.

with the typical location of area KO, although no specific identification of the KO region by means of kinetic borders was made. (These studies used random-dot stereograms containing no monocular cues to the stereoscopic shapes, so the stereoscopic structure was purely cyclopean and invisible monocularly.) Furthermore, studies of illusory contour stimuli of the figure-ground type (Hirsch et al., 1995; Mendola et al., 1999; Larsson et al., 1999; Skiera et al., 2000; Andrews et al., 2002), which typically evoke a strong depth percept, show strong activation in lateral occipital areas overlapping with the region defined as KO. In summary, then, studies with stimuli containing depth structure defined by binocular disparity or by other cues typically show pronounced activation of the lateral occipital region corresponding to that identified as KO. The depth structure in these static stimuli was not defined by moving border shear, implying that activation of the KO region is not restricted to motion-defined stimuli.

In a striking comparison, Tsao et al. (2003) found that responses for a cyclopean random disparity checkerboard (a "relative disparity" stimulus whose depth structure was monocularly invisible) were much greater than for the same stimulus with monocular contours occluding the edge structure (compare their Figs. 4 and 9C, right). The implication is that the border segmentation implicit in the stereoscopic checkerboard stimulus is a much stronger component for the lateral occipital activation than are the local disparity changes per se, supporting the suggestion of Zeki et al. (2003) that the key feature for the KO region may be the generic border structure of the disparity contours, although neither study provides a definition for the KO region in terms of a kinetic contour localizer.

Classification of responses in the KO region requires clear definition of nearby retinotopic areas. In specifying the retinotopic landmarks in the region of V3A, for example, there has been a substantial level of disagreement among the various groups. All agree that this retinotopic region has a 180° representation of the

contralateral field. However, retinotopic stimuli of rotating wedges reveal strong retinotopic activation in the regions lateral to this dorsal foveal response, implying that there is a second retinotopic region that shares the same foveal confluence, termed V3B (Smith et al., 1998; Press et al., 2001). On the other hand, both Smith et al. (1998) and Zeki et al. (2003) identified V3B as being the same area as KO, on grounds of the similarity of its Talairach localization and responsiveness (without employing retinotopic criteria, however). The Harvard group (Hadjikhani et al., 1998; Malach et al., 1995; Sereno et al., 1995; Tootell et al., 1995, 1996, 1997, 1998a,b; Tsao et al., 2003) has not recognized a separate V3B area but designates all the cortex lateral to area V3A as being incorporated into the "V4d topolog", which is defined topologically rather than functionally as the region of cortex connecting the boundaries of V3A, V7 and V5 (hMT+). Thus, their V4d topolog would incorporate both V3B and the KO region, regardless of whether they are separate or coextensive areas.

For the present study, we follow Press et al. (2001) in designating area V3B on the basis of its full retinotopic response characteristics and to define the KO region as lying between retinotopic V3B and the motion area V5 (hMT+) and responding to motion-defined structure in contrast to uniform motion (kinetic contours). It will be seen that, in some hemispheres, this specification defines a KO region adjacent to retinotopic V3B, whereas, in others, it is distinctly separated from V3B. Tootell et al. (1998a) further defined a retinotopic area V7 lying adjacent and dorsal to V3A, including at least a dorsal quadrant, which Press et al. expanded to include a full hemifield.

Having identified this cluster of dorsal retinotopic regions V3A, V3B, V5 and V7, the objective of the study is to evaluate the relative responsiveness of the KO region to a variety of motion, depth and contour stimuli. This goal requires us to distinguish among three hypotheses of the principal function of the KO region, in comparison with its neighboring retinotopic and motion-sensitive regions. These hypotheses are:

1. The original concept of Van Oostende et al. (1997) that KO is specialized for motion-defined contours.
2. The Zeki et al. (2003) hypothesis that KO is specialized for contours in general.
3. The new hypothesis that KO is specialized for encoding depth structure, whether derived from motion cues, figure-ground segregation or binocular disparity.

Materials and methods

Stimuli

To determine the response of the KO region to more general aspects of structure, we used a variety of stimuli corresponding with the different components of the kinetic border stimuli in order to test which of its perceptual properties were responsible for the activation of the KO region (Fig. 1). These stimuli were:

A. a standard kinetic contour localizer consisting of motion-defined contours (Van Oostende et al., 1997), which evoked a strong depth percept of a set of bars standing out in front of a background; the null field consisted of uniform transparent motions at the same rate as the interleaved motions generating the bars in the test field;
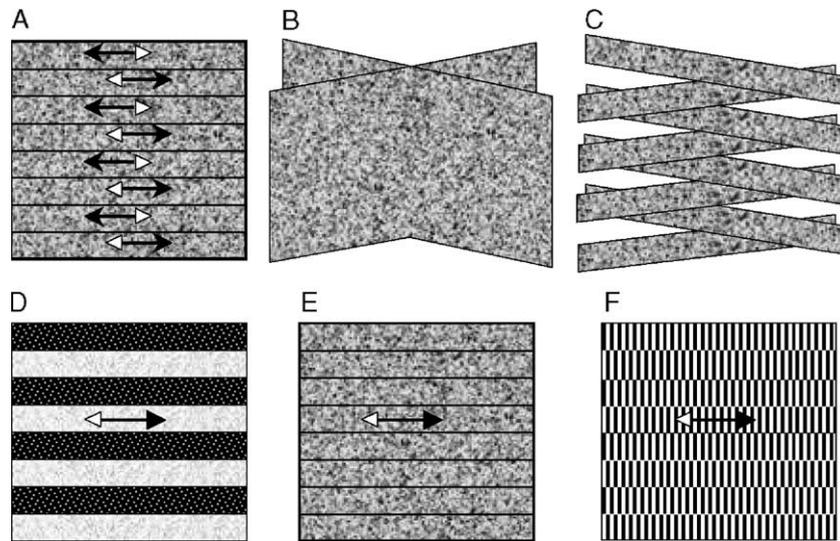
Fig. 2. Depiction of the principal test stimuli for the KO evaluation. (A) Kinetic contour localizer consisting of a random-dot field of alternately moving strips (versus uniform motion). (B) Dynamic random-dot stereogram of intersecting planes (versus a single plane). (C) Dynamic random-dot stereogram of intersecting strips (versus a single plane). (D) Stripes of luminance generated by varying dot density in a random-dot field (versus a uniform random-dot field). (E) Thin dark line contours in a random-dot field (versus a uniform random-dot field). (F) Phase contours in a high-frequency square-wave grating (versus a uniform grating of matching stripe width). Stimuli D–F moved sinusoidally back and forth (arrows) parallel to the contours in the same fashion as the individual motions for stimulus A.

B. a dynamic-noise stereogram of two disparate slanted planes alternating with a single-plane null stimulus[1] to evoke a change in depth percept with no border structure; there is no differential motion component to these stimuli because dynamic noise continues through both intervals;

C. a dynamic-noise stereogram of disparity-defined borders vs. a uniform slanted plane stimuli to evoke a percept of stereoscopic depth borders with the same bar width as for the kinetic border stimulus (A); again, the motion component of these stimuli is balanced because dynamic noise continues through both intervals;

D. luminance bars consisting of 90%/10% density variation of the random-dot field with the same bar width as for the kinetic border stimulus (A); the whole field moved uniformly parallel to the contours but in the same fashion in the test and null intervals;

E. luminance-defined contours (thin dark lines in a dense random-dot field) that evoked no depth percept; the whole field moved uniformly parallel to the contours of the test stimuli and in the corresponding fashion in the null interval;

F. second-order phase contours generated by 180° phase shifts in a square-wave grating, which generated a strong sense of illusory

contours but evoked no depth percept; as in E, the whole field moved uniformly parallel to the illusory contours in the test interval and in corresponding fashion in the null intervals;

G. a standard motion localizer stimulus consisting of a field of low contrast dots forming flow fields alternately expanding and contracting at a rate of 0.5 Hz, with a null field of static dots.

The first six stimuli are depicted in Fig. 2. All stimuli had a mean luminance of 12 cd/m². Stimuli A–E were based on random-dot fields 30° in height with a dot size of 10 arcmin and a mean density of 0.1. The kinetic contour localizer (stimulus A) was a field of 600 × 400 random dots at 10% density in a 32° field organized into 16 stripes moving alternately in opposite directions. The motion of each stripe was sinusoidal, rocking back and forth parallel to the border between the stripes with a frequency of 0.33 Hz and a total extent of 2.2°. The maximum velocity in this motion was thus 2.3°/s. This test stimulus was alternated with a null phase of transparent motion fields at the same velocities (Van Oostende et al., 1997), generated by setting the two moving random-dot fields in alternate lines of the 400-line display (two pixels per line).

The stereoscopic stimuli were formed from two intersecting stereoscopic planes, with the object of providing a stable convergence target at the foveal fixation point and approximate scaling of the disparity difference between the planes with horizontal eccentricity. Depth was readily seen from just outside the central vertical all the way to the peripheral regions of the displays.

For all those stimuli with a bar structure (A and C–F), the spatial period of the bars was 3° (0.33 cy/degree). The null stimulus for the two stereoscopic stimuli, B and C, was a uniform plane of dynamic noise. Stimuli D–F had the same motion in both the test and the null intervals, i.e., uniform sinusoidal motion with the 0.33 Hz period. This motion was designed to increase the activation of the neural generators without providing a differential motion signal among conditions. For stimuli A, D and E, the null stimulus was a uniform static noise field of the same mean density as the test stimulus, while

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[1] The stereoscopic stimuli were generated as dynamic-noise autostereograms with a noise repeat period of 5°. Dual red and green fixation squares on either side of the center of the display provided the fusion target. When fused, it appeared as a central brown binocular fixation square flanked by monocular red and green squares. At the 20 cm viewing distance of the display, divergent fixation was easy and convergent fixation was difficult. The order of the monocular colors provided the feedback that the correct fusion had been obtained. The observers were practiced at obtaining fusion at the correct viewing distance before scheduling their scans and reported when they had obtained fusion at the beginning of each run and whether they had maintained fusion during the run. Any run in which fusion was lost for more than 2% of the duration was excluded from further analysis.

for stimulus F it was a uniform grating matching the base grating in the test intervals. All four of these nonstereoscopic stimuli alternated the stripe orientation between horizontal and vertical at twice the period of the test/null alternation to avoid adaptation to either the stripe orientation or the motion direction (only the horizontal orientation is depicted in Fig. 2).

Perceived depth calibration

The set of stimuli generated for this study was designed to provide controlled presentation of contour structure without depth, depth structure without monocular contour structure and depth without contour structure. However, perceived depth is not simply a matter of stereoscopic disparity but is affected substantially by monocular contour cues. To quantify the amount of perceived depth in our stimuli, they were evaluated in a metric depth estimation procedure (Likova and Tyler, 2003) by each observer tested in the main study by estimation of the mean perceived depth in millimeters over four repeats of a 9-s presentation of each stimulus type. The mean perceived depth over the stimulus area and time, together with the error terms for each stimulus type (including the retinotopic localizers), are tabulated in Table 1. It may be seen that, although the stereoscopic stimuli (B and C) were the most effective in generating depth percepts, a substantial degree of depth was perceived in the kinetic contour stimuli (A) and inconsistently in the retinotopic wedge and ring localizers (which also had relative motion between strips of checks). The remaining stimuli (D–F) were universally perceived as virtually flat, providing strong luminance contour cues of various types together with good control for the absence of depth cues (in contrast to pronounced depth of the kinetic contours).

Scanning procedure

The fMRI responses were collected with 2D spiral acquisition from a custom occipital surface coil in a GE Signa 3 T scanner. There were 23 coronal slices at 3 s TR, with TE of 30 ms and flip angle $70°$, providing $2 \times 2 \times 3$ mm voxels through the occipital cortex. Test and null stimuli alternated for 9 s each in 18 blocks per scan. The stimuli were rear-projected onto a translucent screen inside the bore of the scanner by means of an LCD projector controlled by a Macintosh computer. The observer's head was stabilized by chin and forehead tape, with the eyes looking into a $45°$ mirror to view the front of the projection screen. For the motion stimuli, the observer's task was to maintain fixation on a red 4×4 pixel fixation point at the center of the stimulus and to concentrate on the stimulus pattern. For the autostereoscopic stimuli, the task was to free-fuse with $5°$ divergence on the dual fixation dots to obtain a fused image of the relevant depth percept in the dynamic noise during the test phase or the flat dynamic noise plane during the null phase of the stimuli. No motor task was imposed in order to avoid distracting attention from the relevant stimulus features.[2]

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[2] Note that attention cannot be drawn differentially to a brain area that is not involved in processing the stimulus. All the present stimuli involved test epochs that had more structure than the null epochs, and therefore all should have had the same pattern of activation on the basis of attention. A differential pattern of activation across the cortical surface in two or more conditions thus implies differential processing related to the stimulus properties rather than the activation of a unitary attention mechanism.

Table 1
Mean perceived depth (cm) in the stimuli

	A	B	C	D	E	F	Wedges	Rings
Mean	*0.52	*3.55	*4.36	0.05	0.01	0.02	0.14	0.04
σ	0.17	1.15	1.22	0.11	0.08	0.05	0.60	0.18

$n = 7$; * = significant at $P < 0.01$.

Data analysis and visualization

A high-resolution anatomical (T1-weighted) 3D MRI volume scan of the entire brain was also obtained for each observer (voxel size $= 0.94 \times 0.94 \times 1.2$ mm). Gray (cortex) and white (nerve fiber) matter manifolds were segmented for each observer using publicly available software (Teo et al., 1997). The differential fMRI activity profile was then mapped directly onto the cortical manifold to allow visualization of the response properties over complete cortical areas. The boundaries of the retinotopic projection areas V1, V2d, V2v, V3d, V3v and V4 were established as described in Engel et al. (1997). Retinotopic projection areas V3A, V3B and V7 were specified in accordance with Press et al. (2001). The V5/MT+ motion complex was identified using a full-field expanding and contracting motion vector field of white dots on a black background, alternating with static dots. The classic KO region was defined as an ROI lying in dorsolateral occipital cortex between areas V3B and V5 responding significantly in each voxel to the kinetic contour localizer (Fig. 2A).

The fMRI (BOLD) response was analyzed by extracting the Fourier fundamental of the time series at every voxel at the stimulus alternation rate of 1/18 Hz. The initial response transient to stimulus onset was excluded by beginning dummy visual stimulation 9 s before the experimental stimulus sequence was initiated. A statistical correction for multiple occurrences was applied to the criterion for significant response, in terms of the amplitude of the Fourier fundamental. A coherence level of 0.47 provided a significance level of $P < 0.00005$ in each voxel or a corrected level of $P < 0.05$ per 1000 voxels. Responses below this level do not represent significant activation in amplitude terms, although analysis of the phase vector was implemented under the assumption that there was activation in each retinotopic voxel, but the goal was the best estimate of its phase. This procedure allowed the phase to be used down to a coherence level of 0.3 ($P < 0.01$ in each voxel) for the regions of interest (ROIs) defining visual projection areas from the retinotopy scans, for the motion localizer, and for the classic KO localizer (see Fig. 3). Mean response amplitudes were then averaged across hemispheres for all pairs of ROIs.

To determine the significance of the activation within each ROI and condition, the data were analyzed at an anharmonic submultiple of the block-repeat frequency (10 vs. 12 cycles per scan), which provides an estimate of the non-stimulus-related noise level during the recording conditions. All ROIs $\times$ stimulus type conditions were then entered into a one-way analysis of variance (ANOVA) followed by planned comparisons of the activation at the signal and non-signal block-frequencies at a significance level of $P < 0.01$.

The normalized averages were then subjected to a two-factor ANOVA on ROI and stimulus condition in six groups: stimuli A through F above. Within each analysis group, mean responses for each ROI underwent a post-hoc analysis of planned comparisons,
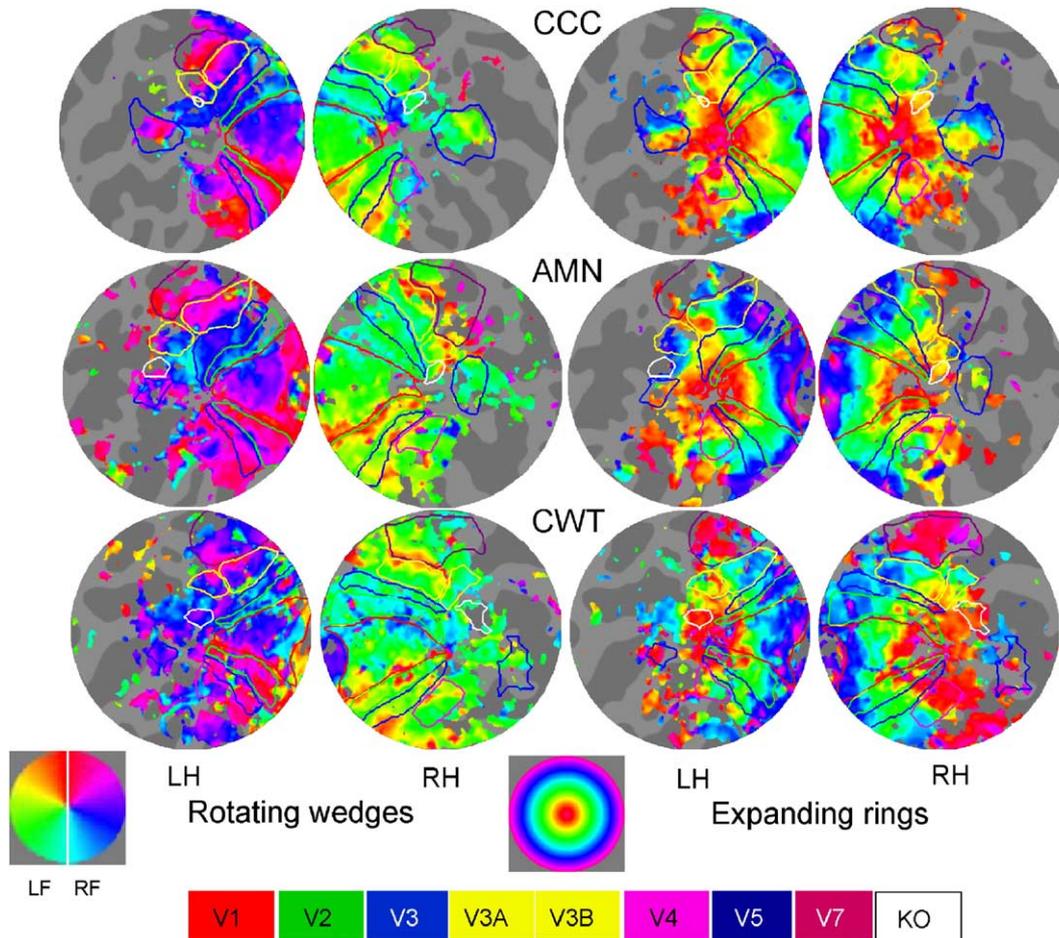
Fig. 3. Retinotopic activations for rotating-wedge stimuli (left columns; meridional color map segregating left field, LF, and right field, RF, stimulation) and expanding-ring stimuli (right columns; concentric color map) for three observers. Activations blurred by a 3 mm volumetric Gaussian kernel for visualization. Retinotopic area boundaries are defined by consideration of the response phase (inset) jointly for the meridional (rotating wedges) and eccentricity (expanding rings) maps and colored according to the color bar. The eccentricity scale is logarithmic from 0.375 to 24°. Small differences among observers are expected in the phase maps due to both differential retino-cortical mapping parameters and different hemodynamic delays.

to determine which ROIs and response types were responsible for the significant main effects, at a significance level of $P < 0.01$ with correction for multiple comparisons.

Correction for self-definition

In the procedure of defining ROIs for noisy data, it is widely understood that the signal in an ROI is likely to be higher for the data set defining the ROI than for subsequent data sets in which the ROI is defined by a prior scan. This bias is generally assumed to invalidate the signal estimation from conditions in which the ROI is defined. However, it can be shown that the bias is as little as 10% for typical ROI estimation conditions. We derived this estimate using Monte Carlo simulation, under the (conservative) assumption that the response profile has a Gaussian amplitude function, which is about the shallowest plausible slope from the center of peak activation in a local cortical activation region. For the simulation, we set the statistical criterion level for the definition of the simulated ROI to $P < 0.01$ for individual voxel activations (equal to the level we adopt in practice for the ROI definition) and the ROI peak activation to twice the criterion level, which is the typical strength observed for scanning durations we employ (~15 min of combined scans per condition).

Under these conditions, Monte Carlo simulation shows that the self-bias, for the activation of an ROI defined in the same scans as the activation, varies with ROI size from an overestimation ratio of only 1.2 for an ROI of 50 voxels in area to a ratio of 1.05 for an ROI of 2000 voxels in area. These are small deviations in relation to the significant ratios of activated to non-activated signals, which are factors of 2–5 times for the ROIs reported here. Moreover, it is straightforward to correct the measured activation in the scans that define the ROI to the value that would be expected if the ROI had been defined in separate scans. Such corrections, based on the individual size of each ROI, were applied to the activations for the V5 and KO ROIs since both types of activation were measured in the scans for which the ROI was defined.

Observers

The same seven observers were scanned in all conditions, five male and two female ranging in age from 32 to 60. They all had normal or corrected-to-normal vision, wearing prescription goggles in the scanner in the latter case. All had normal stereopsis assessed by the criterion of rapid perception of random-dot

Table 2
Talairach coordinates for the KO region

Coordinate	L			R		
	x	y	z	x	y	z
Mean	−35.3	−80.8	5.0	31.7	−84.7	2.5
SEM	7.1	5.8	5.1	4.1	6.1	5.2

stereograms and of perceiving depth structure with free fusion in the MRI scanner projection system.

Results

Examples of the definitions of the retinotopic areas and functional areas KO and V5 (hMT+) are shown for three of the seven observers in Fig. 3 at a coherence level of 0.3 (see Materials and Methods). The two left columns depict flattened occipital maps centered near the occipital pole for the left and right hemispheres, oriented as if viewed from the rear of the brain, together with the activation pattern of the rotating wedge stimulus that defines the projection of the retinal meridians. The two right columns depict the activation of the expanding rings defining the eccentricity mapping in the same format. For each retinotopic area, its approximately radial boundary is defined by the rotating wedge phases (left columns; meridional map coded from cyan to orange for a 180° map such as V1, V3A, V4 and V7). The center-to-peripheral extent is defined by the expanding ring phases (right columns; coded from deep red at 0.375° in the central foveola by six doublings to blue at 24° in the periphery).

Area V7 (dorsal magenta outlines) is a special case in which the meridional and eccentricity phases appear to run parallel to each other. Although it is difficult to interpret this behavior, the parallel structure seems to be a consistent feature and is taken as the signature characteristic of V7 (Tyler et al., 2005a). Moreover,

it is clear that the activity extends through the full range of wedge phases (Fig. 3, left panels), matching the color gamut of V1 in each hemisphere. This result implies that V7 incorporates the full hemifield, not just the quadrant proposed by Tootell et al. (1998a).

Area V3B is designated as retinotopically activated cortex in the lateral direction from the foveal focus of V3A (orange spot dorsal to V3d in the right panels of Fig. 3). We find (Tyler et al., 2005a) that the foveal-peripheral eccentricity phases typically run inferior–superior in the V3B region, roughly perpendicular to those for V3A and adjacent regions of interest (ROIs). Although unexpected, this rotation is the only way to account for the strong retinotopic activation in this region adjacent to V3A (assuming that V3A has a single cycle of foveal-peripheral mapping).

The KO region was defined by the activation to the kinetic contour localizer stimulus (Fig. 2A) in lateral cortex lying between areas V3B and V5. The mean Talairach coordinates and their standard errors (SEM) for this area are specified for the left (L) and right (R) hemispheres in Table 2. It can be seen that these coordinates specify a location substantially posterior to V5 in each hemisphere, which typically has a y coordinate of about −70 mm, and consequently closer to the midline (i.e., x coordinate values smaller than the 45 mm typical for V5).

The full data set of activations for the kinetic contour study is plotted in Fig. 4 for the cortical areas corresponding to those depicted in Fig. 3 (which were specified in terms of the activations in the original voxels in the inplane slices of the fMRI acquisition) to allow qualitative assessment of the results. In overview, the leftmost panel illustrates the response to the kinetic contour localizer, which is expected to give largest response in the KO region defined by this stimulus (although the response amplitude was corrected for bias in the self-definition of the ROI as described in Materials and Methods). However, the third panel shows that the response to the
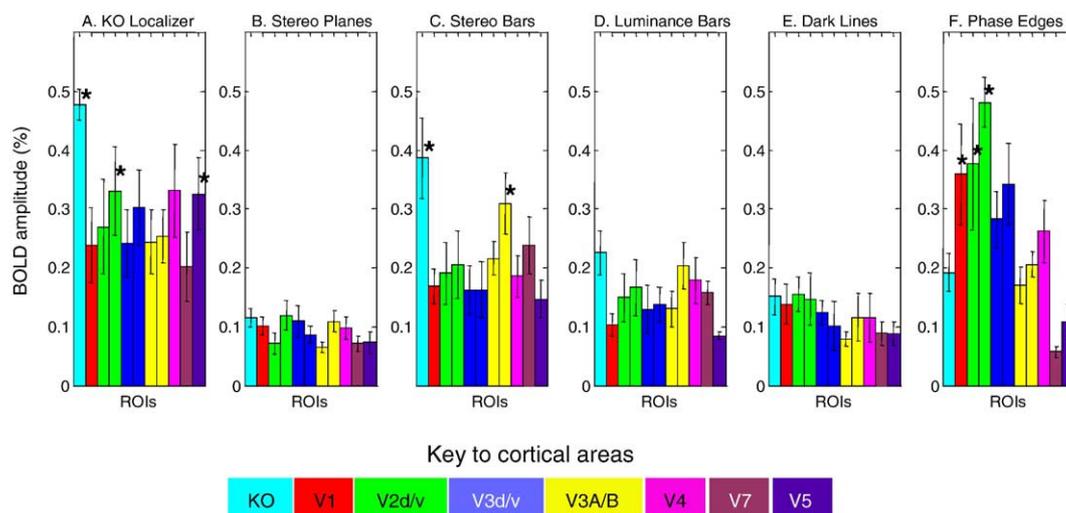

Fig. 4. Mean percent BOLD amplitudes for the seven observers in each inplane ROI for all stimulus conditions combined across hemispheres. Asterisks indicate significant activation relative to the anharmonic analysis of the same signals (see Materials and Methods). Colors represent ROIs specified in order in the color key, where d and v indicate dorsal and ventral partitions of the cortical areas, respectively. Other than its localizer (stimulus A), the only significant response for the KO region (first bar in each panel, in cyan) is for the stereo structure stimulus (C). The other kinds of edge stimuli (D, E) produced little response in any area (D, E), except for the illusory phase contours (F), which elicited no depth percept but produced an entirely different activation pattern, with strong responses in areas V2d, V2v and V3d but not in the KO region.

stereoscopic structure stimulus is not significantly lower in the KO region than its defining localizer and is significantly larger than in all retinotopic areas except V3B. Note that the largest retinotopic response to the stereoscopic structure stimulus, in area V3B, is in general agreement with the finding of Backus et al. (2001) in the same region (although they included this region under the V3A designation). In detail, however, the stereoscopic plane stimulus is the one most similar to their two-plane stimulus, but it fails to show any significant response in any of the defined ROIs (third panel of Fig. 4). The data therefore suggest that the response to disparity per se is weak everywhere in the cortex but that the response to stereoscopic structure in the form of sharp disparity edges generates greater activation in V3B than the earlier retinotopic areas, culminating in the largest response in the region designated as KO.

Mean activations in retinotopic ROIs are evaluated through the F test, specifying the probability level (P) and degrees of freedom (df) for each test. The analysis was conducted at four levels:

1. a one-way ANOVA for activation in all ROIs in all stimulus types at both the analysis block-frequency and an anharmonic submultiple of this frequency to determine the prevailing noise level;
2. a set of planned comparisons for the signal and noise activations in each ROI based on the Tukey–Kramer criterion at a significance level of $P < 0.01$, for which the significances are indicated by the asterisks in Fig. 4;
3. a two-way ANOVA for ROI × stimulus type (given that the first two tests were significant); and
4. a set of planned comparisons over the ROIs based on the Tukey–Kramer criterion at a significance level of $P < 0.01$. All significant differences among ROI activations are listed in the final column of Table 3.

The complete statistical analysis of the data set provided in Table 3 shows that there was a significant main effect of both ROI ($F_{10} = 5.09$, $P < 0.0001$) and stimulus type ($F_5 = 35.83$, $P < 0.0001$), together with a significant interaction ($F_{50} = 2.12$, $P < 0.0001$). Planned comparisons with an adjusted significance level of $P < 0.01$ revealed that activation of the KO region was significantly greater for the kinetic contour localizer than for all three types of non-

Table 3
Statistical analysis and post-hoc comparisons among stimulus types A–F

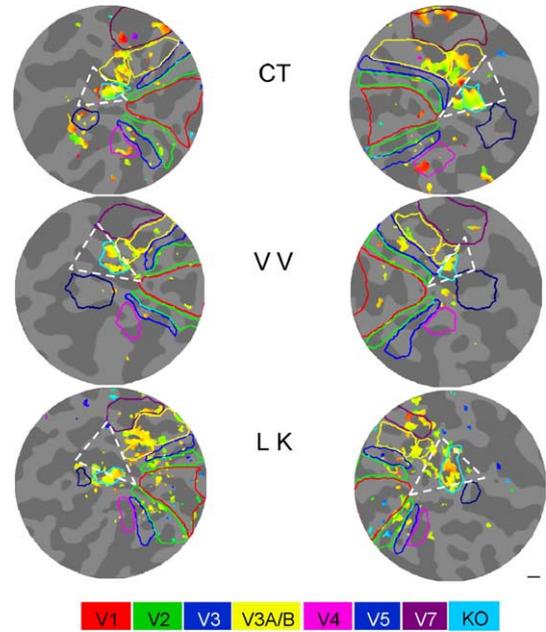| ROI	F	P	df	Comparisons
All one-way	5.09	<0.0001	65	
Two-way	4.60, 35.83	<0.0001, <0.0001	10, 5	
Two-way Int.	2.12	<0.0001	50	
KO	13.67	<0.0001	5	A > C–F, B > C, E
V1	4.23	0.005	5	F > C, D
V2d	2.80	0.034	5	ns
V2v	7.23	0.000	5	F > B–D
V3d	5.30	0.001	5	A > B, D
V3v	4.12	0.006	5	ns
V3A	2.98	0.027	5	ns
V3B	5.04	0.002	5	F > C
V4	3.42	0.015	5	ns
V7	4.89	0.002	5	B > F
V5	8.60	<0.0001	5	A > B–F

Fig. 5. Examples of flattened occipital lobes showing retinotopic areas V1–7 and functional areas KO and V5 (see color bar), together with the activation pattern for the stereoscopic contour stimulus (stimulus C) above a coherence level of 0.5. Activations blurred by a 3 mm volumetric Gaussian kernel for visualization. The color of the activation represents response phase, where yellow is a phase of 90° (4.5 s delay). Stereo activation is strong in the KO region (cyan outlines) and scattered in area V3A and V3B (yellow outlines) with little activation elsewhere in either retinotopic or lateral occipital cortex. White dashed triangles delineate the specification of the V4d topolog (Tootell and Hadjikhani, 2001). Calibration marker represents 1 cm.

motion contours. This result validates the specificity of a dorsolateral occipital region for kinetic contours and does not support the contention of Zeki et al. (2003) that this area is equally responsive to contours of other types. In particular, the border structure of phase-border stimulus closely resembles the phase boundary in their color contour stimulus, although ours was achromatic. (We did not test an exact duplicate of their (colored) stimulus because the goal was to evaluate the concept of generic contour responsiveness rather than replication of their particular stimulus design.)

The responses to kinetic strips and to stereoscopic strips were statistically equivalent, even though the kinetic contour stimulus is the one for which the KO ROI was defined. (Note that the activations in areas that they defined were corrected for self-definition according to the procedure described in Materials and Methods.) Moreover, none of the primary retinotopic areas or V5 (hMT+) participated significantly in activation to either the disparity structure or planar disparity stimuli. Table 3 shows that the only other area with a significant response specificity for stereoscopic stimulation was retinotopic area V7, in which stereoscopic contours were preferred over the phase-contour stimulus. However, the function of V7 is clearly distinct from that of the KO region because V7 did not show significant activation to the kinetic contour localizer stimulus. The V7 function is also clearly distinct from that of both V3A and V3B, neither of which was significantly activated by either of the stereoscopic stimuli at the statistical criterion of the overall analysis (although V3B did show significant activation relative to the estimated noise level on the individual analysis of Fig. 4).

The retinotopic eccentricity of the KO region was specified in terms of the sinusoidal component of the expanding ring response cycle; the average phase for our seven observers in the two hemispheres was 0.77 ± 0.5 radians. The expanding rings were incremented in log steps of factors of 2 from $0.375°$ to $24°$ eccentricity. In this metric, the average eccentricity of the peak kinetic contour response has a geometric mean of $0.66°\pm 0.25°$.

Examples of the ROIs and stereoscopic depth-contour activations for left and right occipital lobes of three observers are shown in Fig. 5 for a flattened region centered at a location half-way between foveal V1 and V5 (hMT+). The medial surface of each occipital lobe (inner halves of maps) contains the primary retinotopic areas with the occipital pole at the tip of area V1 (red outline). The KO region is indicated by the cyan outline, derived as enclosing the largest region of activation for the kinetic contour localizer that fell between areas V3B and V5. The patches of yellowish color show the activation by the stereoscopic contour stimulus. The only consistent activation in lateral occipital cortex is within and near the KO region. Patchy activation is also visible around retinotopic areas V3A, V3B and V7, in some cases, but it is clear that the most consistent focus of activation by stereoscopic contours is in the region designated as KO (cyan outline).

Discussion

In the retinotopic hierarchy, the first area to show a consistent response to the disparity structure stimuli was V7 (Table 3). (The patchy activation in areas V3A/B shown in the examples of Fig. 5 did not reach statistical significance in the full analysis but was supported by the individual analysis of Fig. 4.) However, Table 3 indicates that V7 did not show a significantly stronger response to *kinetic* contours than to any other stimuli, with or without contours. Thus, for the present stimulus set, V7 shows the greatest preference for the disparity structure per se but is responsive neither to contours in general nor to the depth or the kinetic aspects of the kinetic contour stimulus. Moreover, in common with all other defined areas, V7 shows very little response to the same disparity in the absence of depth structure. This result implies that V7 has a specialization for depth structure conveyed by disparity information. (The same conclusion applies to V3B in the individual area analyses of Fig. 4.) This is an interesting result in light of several neurophysiological studies showing that a large proportion of neurons in the intra-occipital sulcus at the junction between occipital and parietal cortex are selective for stereoscopic surface orientation (Shikata et al., 1996; Taira et al., 2000; Tsutsui et al., 2001, 2002). This anatomical structure is the sulcus underlying retinotopic area V7. Corresponding activation in the human intraparietal sulcus has been found for a task of surface orientation discrimination (Shikata et al., 2001).

The cortical area known as KO, on the other hand, shows a similar response for the kinetic contours and the stereoscopic contours. Because the kinetic contour stimulus generated a strong impression of depth structure, this pattern of behavior suggests that the KO region responds to the property in common between the two stimulus types, which is the *depth* structure of the borders perceived in both stimulus types, rather than being specific for kinetic borders alone (Table 3). Conversely, the KO region shows no significant response to either type of luminance contours or to illusory phase contours (which evoked no percept of depth

structure, as quantified in Table 1), so this region cannot be specialized for contours as a class. (Previous studies reporting responses in the KO region to luminance contours did not control for their degree of depth percept, as was done for the present stimuli.) Our data do not, however, establish that individual neural circuits in this region represent the depth structure in a cue-independent fashion since these circuits are below the resolution of fMRI.

It is important to note that the KO region does not respond either to simple disparity or to depth per se. The disparity plane stimulus (B), with minimal depth structure, generated the lowest response of any stimulus in this region (and indeed in all the other designated cortical areas), as shown in Table 3 and Fig. 4, with no cortical area showing a significant signal/noise ratio for stimulus B. This distinction establishes that the significant response to depth structure (stimulus C) is not attributable to its relative depth relations (cf Tsao et al., 2003), which were well matched to those of the transparent planes of stimulus B, but to the spatial structure of sharp boundaries between different depth segments. The measures of perceived depth (Table 1) assure that the transparent planes of stimulus B were evoked almost the same large degree of perceived depth separation as the intersecting ribs of stimulus C ($\sim$4 cm). The strong preference of the KO region for stimulus C over stimulus B makes it clear that it is the depth *structure* rather than the net disparity or relative depth per se that is the relevant feature for its activation. Moreover, the equally strong activation for the kinetic stripes (stimulus A) implies that perceived depth is not a strong determinant of the response since the perceived depth of stimulus A, though definite, was less than a tenth of that for stimuli B and C (Table 1). We conclude that the KO region is best regarded as a primary center for the representation of depth structure, independent of the visual modality with which the depth is specified or even the quantitative degree of depth. Any study evaluating the contour specificity of this region needs to take the degree of depth structure evoked by the chosen stimuli before the role of contours per se can be distinguished from the depth representation.

Reconsideration of the KO designation

In view of its retinotopy and of the strong response to depth edges in the absence of relative motion, we suggest that the KO (kinetic occipital) designation for this region is inappropriate. It may be premature to propose that it be renamed as a specific architectonic area, but it appears that this cortical location is more likely to be processing cue-independent depth structure than kinetic contours per se. For the purpose of the present discussion, we will designate this region (responding to depth structure and lying lateral to area V3B) the "occipital depth structure" (ODS) region of cortex.

Relation to motion responses

Before proceeding with further analysis of the ODS region, we first consider the negative result for disparity or depth structure responses in motion area V5 (hMT+). In monkeys, motion area MT shows strong responses to stereoscopic stimuli (DeAngelis and Newsome, 1999; DeAngelis et al., 1998; Krug et al., 2004), although stereoscopic responses in the human motion area (V5) are typically weak unless the stimulus incorporates motion (Backus et al., 2001; Tsao et al., 2003). The present

results confirm this weak response (Fig. 4), with V5 showing one of the smallest responses for any ROI to every stimulus condition except the kinetic contour localizer. (In the case of the kinetic contour localizer, the significant V5 response may be attributable to a mismatch in the perceived velocity between the motion strips and the uniform motion of the null stimulus, even though the uniform motion was set to twice the motion of either strip, i.e., matched to the relative velocity. Neurons tuned for a differential velocity in their receptive field, as are many monkey MT neurons (Maunsell and Van Essen, 1983; Allman et al., 1985; Olavarria et al., 1992; Britten, 2004), would show much reduced response to any uniform velocity.) It remains unresolved whether the difference between monkey and human results for stereo processing in motion area V5 is a genuine difference in the locus of processing of stereo signals or a result of the insensitivity of the BOLD signal to differential activation of neural populations within the same fMRI voxel. The strong stereoscopic response in the ODS region may offer some support for the former option since it is close to V5 and may represent a separation of the specialization for stereopsis that is allowed by the increased area of human occipital cortex relative to that for the monkey. (The issue of stereoscopic activation in V5 is, however, a separate topic that has been addressed by the adaptation technique; Neri et al., 2004. In that study, V5 showed a similar strength of adaptation to disparity variation to that seen in dorsal retinotopic areas V3A and V7, but neither the ODS region nor the responsiveness to disparity structure was evaluated).

Retinotopy of the ODS response

One known property of the ODS region is that it has retinotopic specificity when stimulated by a retinotopic localizer stimulus (see Fig. 3). Tootell and Hadjikhani (2001) showed pronounced retinotopy in this region, arguing for a discrete subdivision into central- and peripheral-responsive areas that they designated "LOC" and "LOP", respectively. The ODS region falls roughly within the boundary of their V4d topolog, although it constitutes only a small part of that region. This specialization provides one example of the functional diversity admitted within the definition of the V4d topolog (Tootell and Hadjikhani, 2001), but the occasional mismatches illustrate the difficulties of attempting a topological definition of cortical areas defined by the fMRI methodology. The present data support the idea that the ODS region often shows a strong retinotopic response, with a strong response in the central fovea for expanding ring stimuli and for rotating wedge stimuli near the lower vertical meridian, as illustrated in Fig. 3 (see Tyler et al., 2005a). The ODS region was thus strongly limited to part of the foveal-responsive zone designated as LOC by Tootell and Hadjikhani (2001).

Is the retinotopic response in the ODS region incompatible with the lack of significant response to the luminance bars (stimulus D in Fig. 2)? The answer is no because the retinotopic stimuli are dynamic counterphasing checkerboards that stand out from their uniform-gray background whereas the luminance bar stimuli were generated by density modulation in random-dot fields that moved slowly in both the test and null phases of stimulation. The spatiotemporal contrast of the retinotopic stimulation therefore formed a dramatic contrast modulation relative to the gray field of its null phase, while the luminance bar stimulus consisted of full-contrast dots in both phases — only their spatial arrangement

varied. Added to the contrast modulation is the fact that the retinotopic stimulus evoked a depth percept of the flickering wedge or ring appearing in front of the gray background (Table 1), providing two reasons to expect the retinotopy stimulus to generate much greater activation in lateral occipital cortex than the non-flickering luminance density bars.

It is noteworthy from Fig. 5 that the stereoscopic contour activation covers only a small part of the region designated as the V4d topolog (specified as the white dashed triangles). This localized activation therefore constitutes a specialized subregion of V4d topolog, in line with its known subdivisions specializing in illusory contours and symmetry (Tootell and Hadjikhani, 2001; Tyler et al., 2005b; Sasaki et al., 2005). The phase-contour stimulus (Fig. 2F) was designed as a probe for illusory contour activation with no associated depth percept in contrast to the kinetic contour and disparity edge stimuli (Figs. 2A and B), which both evoked pronounced depth percepts (see Table 1). This probe shows that the ODS region is not a location that is particularly responsive to illusory contours of the phase kind since significant activation for such contours was found only in retinotopic areas V1, V2v and V3B.

Consider, in particular, the specificity of area V3B for this phase contour stimulus. In view of the past confusion between the areas designated as V3B and as KO, V3B needs to be distinguished from the ODS region in both positive and negative senses: in the present data, the ODS region is most responsive to the depth contours (and significantly more so than V3B; Table 3), while V3B is most responsive to the phase contour stimulus (though not significantly more than the ODS region; Table 3). Hence, we propose that retinotopic V3B should be considered as the main region responsive to illusory contours per se, while the ODS region seems to be the area responsive to the depth structure that may accompany the illusory contour percept. For stimuli containing the type of illusory contours that elicit depth segregation and thus also operate as depth contours (Hirsch et al., 1995; Mendola et al., 1999; Larsson et al., 1999; Skiera et al., 2000; Andrews et al., 2002), both areas would be expected to be activated. (Activation would further be expected in additional form areas if the illusory contour stimuli had an organized form relative to their null counterparts.) Thus, the present results showing localized responsiveness of the ODS region to depth structure stimuli are compatible with the more extended activation previously reported for illusory contour stimuli containing multiple cues.

Generic depth specificity

Depth is an important attribute of objects, whose cortical representation is usually studied by contrasting them with flat textures. Such object/texture contrasts activate an extended swath of areas in lateral occipital cortex whose particular specificities remain to be explored (Malach et al., 1995, 2002; Hasson et al., 2003). For example, the activation of object areas by stereoscopic depictions of the objects with monocular contours eliminated (Kourtzi et al., 2002) incorporates the cues of figure/ground organization, perceived depth, contour structure and depth ordering in addition to object identity. In principle, each of these cues could have separate neural processing circuitry. Backus et al. (2001), using transparent plane stimuli, found disparity processing to predominate in area V3A. Their stimuli excluded figure/ground organization, contour structure, depth structure and object identity

but included perceived depth, transparency and depth ordering in addition to the local disparity processing that they intended to study.

By separately isolating the response to generic depth structure from the responses (a) to disparity per se, (b) to disparity-specific relative depth and (c) to non-stereoscopic contour structure, we show that the ODS region is much better characterized as a primary locus of the generic representation of depth structure than as responding to kinetic contours alone or to a variety of non-depth contours. Depth stimuli containing extra information, such as lateral motion, depth motion or recognizable form information, may be expected to activate more extended areas of occipital and parietal cortex, as indeed was reported by Tsao et al. (2003). The only types of contour that activate the ODS region seem to be those associated with perceived *depth* relations since it shows no significant response to line contours or to structure from luminance or second-order cues (Table 3).

Finally, it should be noted that "depth structure" is itself a broad term incorporating a variety of forms of depth encoding, each of which may involve different neural processes. These include

    i) depth edge structure, the sharp edges of sudden changes in depth
    ii) depth segmentation, the presence of defined regions of coherent depth between the depth edges
    iii) depth ordering, the ordinal layering into a succession of depth levels
    iv) depth occlusion, of far by near surfaces
    v) depth form, the shape of the differential depth configuration
    vi) ambiguous alternations of depth structure seen in kinetic depth stimuli.

It will require extended study to isolate the neural representation of each of these properties. Of the listed possibilities, two that can be excluded by the present results are options (iii) and (vi). Depth ordering was present at full strength in the transparent planes of stimulus B, but this stimulus gave no significant activation in the ODS region (or any other region studied), and therefore its depth ordering cannot have played a significant role in the responses obtained. And, although there are alternations of the perceived depth structure in the kinetic contour stimulus (A), there are no such alternations in the stereoscopic structure stimulus (B). Since the activation was quite similar for these two stimuli, the alternations cannot have made a substantial contribution to the response.

Conclusion

The area in lateral occipital cortex that is maximally responsive to kinetic contours also shows strong response to stimuli containing stereoscopic contour structure in the absence of differential motion cues or monocular cues to the structure, but no significant response to unstructured disparity or luminance-based contour stimuli. We therefore conclude that the primary stimulus property activating this areas is the depth structure of the stimuli as opposed to their motion or luminance structure. This cortical area also shows a reliable response to the retinotopic stimulus probe of counterphasing luminance checkerboard stimuli, peaking at an eccentricity of only ~0.7°. The stereoscopic structure response is unique to this area in relation to primary retinotopic areas from V1 to V3, but there is also significant response to the stereoscopic structure stimuli in the dorsal retinotopic area V7 and adjacent regions. None of the areas evaluated showed significant selectivity for relative disparity in the absence of depth edge structure.

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