

Dynamic Shape Integration in Extrastriate Cortex

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Summary

Background: In anorthoscopic viewing conditions, observers can perceive a moving object through a narrow slit even when only portions of its contour are visible at any time. We used fMRI to examine the contribution of early and later visual cortical areas to dynamic shape integration. Observers' success at integrating the shape of the slit-viewed object was manipulated by varying the degree to which the stimulus was dynamically distorted. Line drawings of common objects were either moderately distorted, strongly distorted, or shown undistorted. Phenomenologically, increasing the stimulus distortion made both object shape and motion more difficult to perceive.

Results: We found that bilateral cortical activity in portions of the ventral occipital cortex, corresponding to known object areas within the lateral occipital complex (LOC), was inversely correlated with the degree of stimulus distortion. We found that activity in left MT+, the human cortical area specialized for motion, showed a similar pattern as the ventral occipital region. The LOC also showed greater activity to a fully visible moving object than to the undistorted slit-viewed object. Area MT+, however, showed more equivalent activity to both the slit-viewed and fully visible moving objects.

Conclusions: In early retinotopic cortex, the distorted and undistorted stimuli elicited the same amount of activity. Higher visual areas, however, were correlated with the percept of the coherent object, and this correlation suggests that the shape integration is mediated by later visual cortical areas. Motion information from the dorsal stream may project to the LOC to produce the shape percept.

Introduction

As mobile perceivers in a three-dimensional world, people often encounter instances in which a moving object is mostly occluded by another, for example, a person moving behind a slightly open door. Observers can recover the shape of such a moving object with little trou-

ble, even though the motion hides some parts of the occluded object as it reveals others. The experiments reported here examine how our visual system forms coherent representations of objects when shape information must be dynamically integrated over time. Dynamic integration is as yet poorly understood, and we used functional magnetic resonance imaging (fMRI) to reveal the contribution of early and later visual cortical areas to this process.

The classic paradigm used to study dynamic shape integration is a slit-viewed stimulus [1]. Observers see a moving object that is only partly visible through a narrow slit in an occluding surface. When the observer maintains fixation upon the slit, the translating figure only stimulates a narrow strip of the retina corresponding to the area projected from the slit. Nevertheless, the observer sees a complete figure moving behind the slit, with the visible portion appearing to be wider than the slit [2]. The successive views of the object are integrated "postretinally" [3], and the locus of shape integration has been heavily debated [4, 5]. Thanks to recent functional imaging studies of object and motion areas in visual cortex, we may be able to better define the neural substrates of "postretinal" integration and constrain theories of object recognition.

The experiments we present here examined how the dynamic shape integration task is supported by cortical regions whose functions have been previously defined. Because successful aperture viewing provides a shape percept and a motion percept, we focused on cortical regions important for shape and motion perception, specifically the ventral occipital cortex and the human motion complex, MT+. We also examined early retinotopic cortex to determine the relative contributions of early versus later visual cortical areas to dynamic integration. The portion of the ventral occipital cortex that stretches along the fusiform gyrus has been implicated in shape perception. This cortical area is considered to be the ventral extent of the lateral occipital complex (LOC) that is implicated in shape perception [6–8]. Area MT+ comprises areas that are homologous to the monkey middle temporal (MT) and medial superior temporal (MST) cortical areas [9]. In a slit-viewed object, integration of shape cannot occur without motion, and, thus, for this stimulus, the two aspects of perception are not dissociable. Indeed, one study first proposed for computational reasons that global motion must be computed prior to shape integration; this study then found behavioral evidence supporting their proposed joint computation [10].

We examined the contribution of the LOC and MT+ to the dynamic shape integration task by manipulating the integration process. Successful integration of the aperture-viewed stimulus provides a shape and motion percept, while unsuccessful integration should provide no shape percept and limited motion percept. To manipulate integration, we designed a stimulus that underwent a dynamic distortion as it passed behind the slit (see Figure 1). We used three levels of distortion in the study: undistorted, moderately distorted, and strongly dis-

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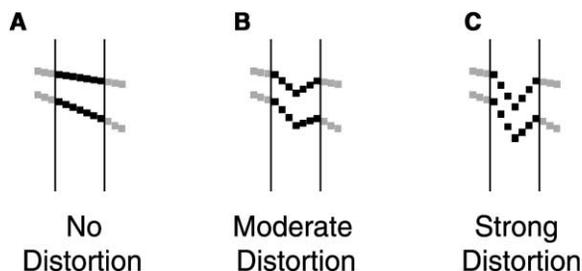


Figure 1. Stimulus Creation

(A–C) There were two levels of distortion: (B) moderate and (C) strong. Phenomenologically, the percept varied with the amount of distortion. With no distortion, the display is exactly the same as the original aperture-viewed object. With strong distortion, the percept of object shape disappears, along with most of the percept of motion: the percept consists of a number of V-shaped lines moving up and down. With a moderate distortion, however, comes an intermediate percept: object shape cannot be perceived to the extent that recognition can occur, but observers can see some shape features. Object motion is also distorted so that the indefinable shape seems to travel down and up through the slit (according to the path of the distortion).

torted. Each view of the object in motion was distorted by shifting the pixels into a “V”. This distortion is similar to one that might be perceived if a movie were projected on a screen that was folded in the center. This effectively introduces high spatial frequency noise into the stimulus. Because the distortion allowed a one to one correspondence between each pixel of the undistorted and distorted stimuli, it maintained all vertical displacements and orientation changes of the line segments [10] within the slit. In addition to these three slit-viewed conditions, we also included a control condition in which a fully visible shape moved in front of the occluders (see Figure 2).

We used these four conditions to test the hypothesis that cortical areas involved in object shape and motion perception would be less active when integration is impaired. We predicted that activity in these areas would be stronger in the undistorted condition than the strongly distorted condition because the distortion would impair both object and motion perception.

Within the same scanning session, we used one independent functional localizer to determine areas of the cortex responsible for motion perception and another to map early retinotopic areas of visual cortex. The fully visible condition was used to localize areas of the cortex involved in object perception.

Our results showed that cortical activity in both object and motion areas was greatest when the slit-viewed stimulus was undistorted and lowest when the stimulus was strongly distorted. In early visual areas, however, cortical activity was equivalent, suggesting that dynamic shape integration occurs at or before the higher visual areas.

Results

Object Area

Within the ventral LOC, an ANOVA found a significant effect of condition ($F[5,35] = 44.79$, $MSe = 0.25$, $p < 0.001$). As Figure 3 shows, activity in the undistorted condition was significantly higher than in the strongly distorted condition, and activity in the moderately distorted condition was in between those two. The analysis also showed that there was stronger activity in the left hemisphere than the right ($F[1,7] = 6.17$, $MSe = 1.07$, $p < 0.042$). This likely reflects the lateralized stimulus presentation. There was no interaction between condition and hemisphere. A linear trend analysis upon the combined object area activity in both hemispheres showed a significant decrease in activity as the distortion increased ($F = 6.51$, $MSe = 0.61$, $p < .01$).

Motion Area

There are three main results of note (see Figure 4). First, a planned pairwise comparison found that activity in the strongly distorted condition was less than in the undistorted condition, but this occurred in the left hemisphere only ($t = 3.14$, $p < 0.05$). The moderately distorted condition elicited an intermediate response, but a linear trend analysis found no significant trend in either the left hemisphere ($F = 2.74$, $MSe = 0.65$, $p > 0.5$) or the right ($F < 1$). Second, in the left hemisphere, cortical response to the undistorted slit-viewed stimulus was

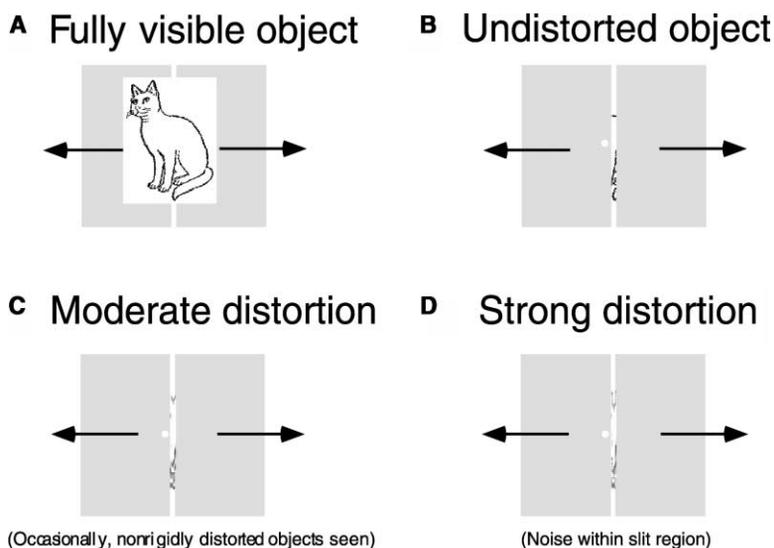


Figure 2. The Four Experimental Conditions
Observers fixated on the white dot to the left of the slit.

(A) The control condition when the line drawing is fully visible.
(B) The classical slit-viewing condition. In this condition, shape is perceived, but is horizontally compressed.
(C) The moderate distortion case in which observers reported seeing some shape and motion but could not recognize the object.
(D) The strong distortion case in which observers mainly reported seeing vertical motion. Observers were unable to see shape.

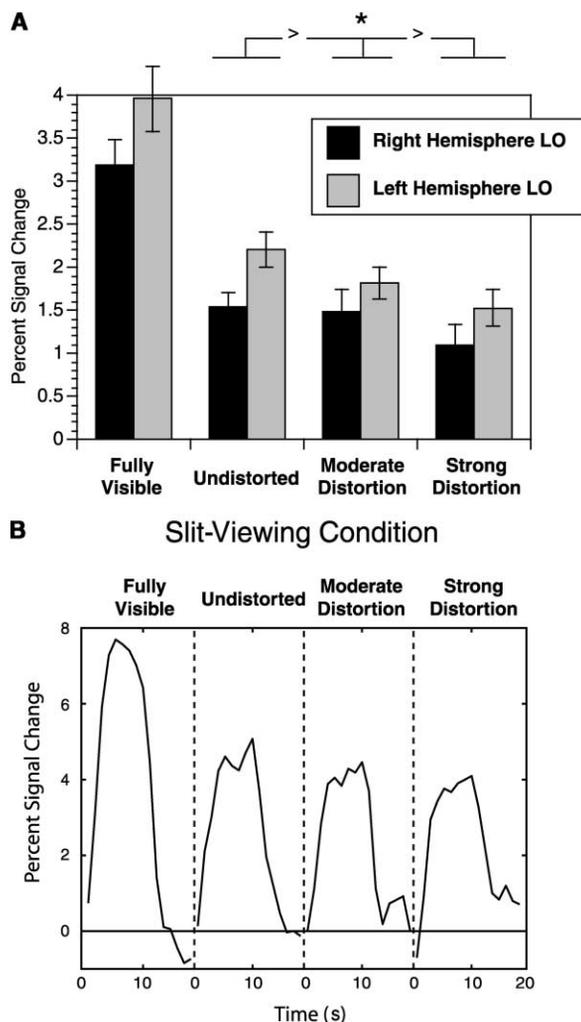


Figure 3. Results in the Ventral LOC

(A) The four experimental conditions. Error bars indicate ± 1 standard error. Activity in the undistorted condition was greater than in the strongly distorted condition, with activity in the moderately distorted condition at an intermediate level. Activity in the fully visible moving stimulus was greater than in any slit-viewed condition. (B) Average time courses for the data used in the analysis of (A). The curves plot mean activity from active pixels in the ventral LOC averaged across all eight subjects separately for each condition.

not reliably different than to the fully visible stimulus. Third, we found that cortical activity was stronger in the left hemisphere for the slit conditions. A 2 (hemisphere) \times 3 (slit conditions) analysis of variance (ANOVA) showed that there was a significant difference between the hemispheres ($F = 12.21$, $MSe = 0.86$, $p < 0.01$), but no overall difference between slit conditions ($F = 2.13$, $MSe = 0.18$, $p < 0.16$) and no reliable interaction ($F = 1.29$, $MSe = 0.06$, $p < 0.31$). The lateralization of MT+ activity is also likely due to lateralized stimulus presentation, which we will further discuss below.

Early Visual Areas

Figure 5 shows that there were no significant differences in activity across the three slit conditions in early retinotopic cortex. This suggests that the activity seen in

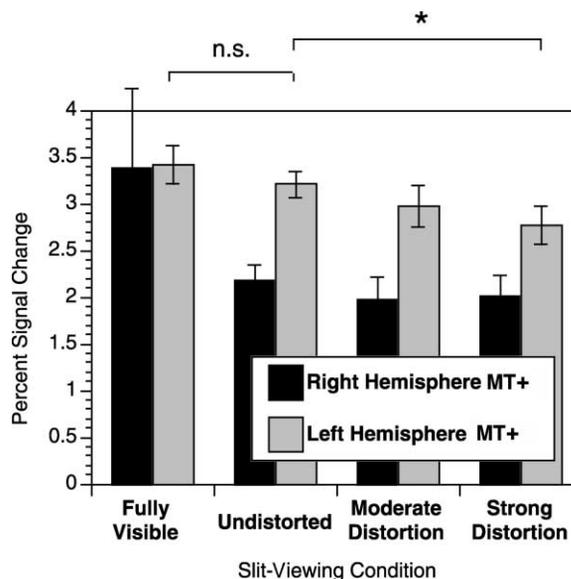


Figure 4. Results in Area MT+

In the left hemisphere, the motion signals in all slit conditions are stronger, and there is no difference in signal change between the fully visible and undistorted slit-viewed conditions. In the right hemisphere, the motion signal from the fully visible moving object is stronger than the slit-viewed objects, and the slit-viewed objects did not elicit different cortical activity.

higher areas does not reflect differences produced by low-level features.

Behavior

Because complex responses are difficult to gather during fMRI, subjects did not perform an object-naming task in the scanner. A separate post-hoc psychophysics experiment conducted outside the scanner, but under similar viewing conditions, verified that the objects were seen and recognized reliably better in the undistorted (93% correct) than in the distorted conditions (26% cor-

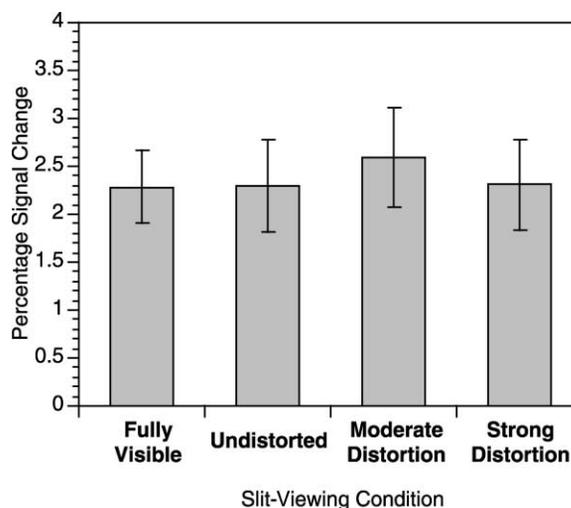


Figure 5. Early Visual Areas

Neural activity was equivalent in all slit-viewing conditions as well as in the fully visible moving object condition.

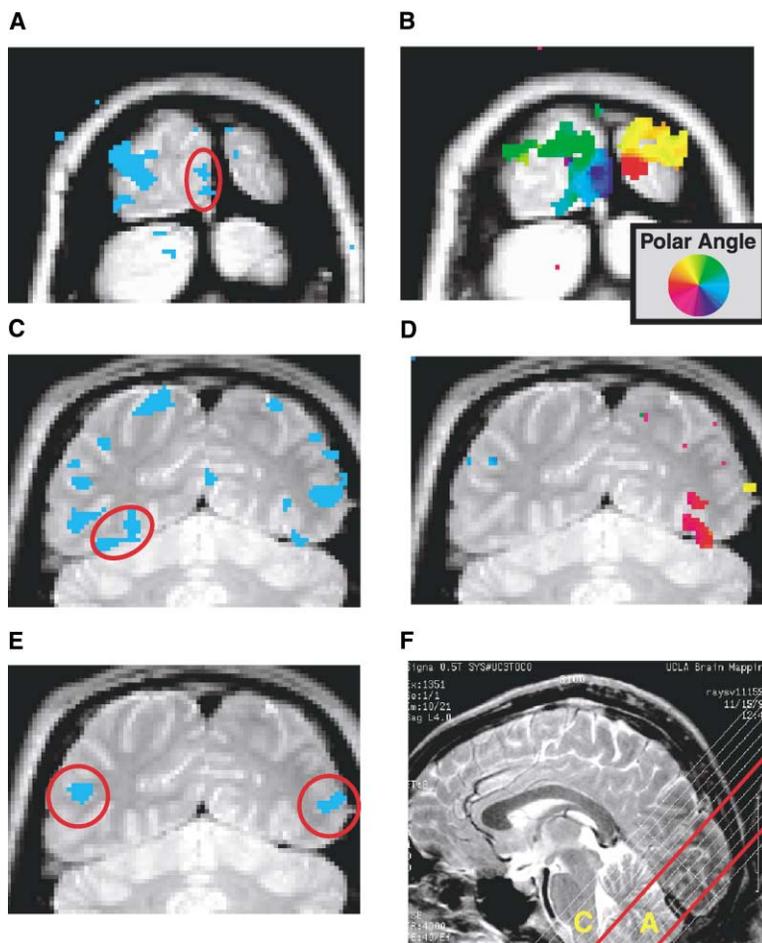


Figure 6. Regions of Interest for a Representative Subject

ROIs are marked in red and were determined by using a combination of anatomical and functional criteria.

(A) Early retinotopic areas were defined as areas showing activity during the moderately distorted slit-view condition (see the Experimental Procedures for details). Voxels exhibiting such activity are shown in blue for a representative subject.

(B) Additionally, early retinotopic ROIs were constrained to contain only voxels showing retinotopic mapping and falling near the calcarine sulcus. The results of retinotopic mapping in the same slice and subject are shown. The color indicates the polar angle within the visual field represented at each voxel. Smooth changes in color indicate retinotopic mapping. The left and right horizontal meridia fall near blue and red, respectively, while the upper and lower vertical meridia fall near green and purple. The ROI shown in red in (A) falls clearly within the retinotopic region shown in (B).

(C) The ventral area LOC was defined as areas that showed activity during the fully visible object condition. Voxels showing such activity are shown in blue.

(D) Additionally, the LOC was constrained to contain only voxels not showing retinotopic mapping along the ventral occipital lobe and posterior temporal lobe. The panel shows results of retinotopic mapping in the same slice and subject.

(E) Area MT+ was defined as an area on the lateral aspect of the occipital lobe that showed greater activity during moving rings than stationary rings. Voxels showing such activity are shown in blue. Additionally, MT+ was constrained to contain voxels not showing retinotopic mapping.

(F) The slice prescription for this subject. The slices shown in (A)–(E) are indicated in red.

rect in the moderate and 21% in the severe distortion conditions). Subjects also rated the strength of perception of both global (horizontal) and local (vertical) motion using a 5-point scale. Average ratings of global motion strength decreased reliably as distortion increased (from 4.8 in the undistorted condition to 3.3 in the moderate and 1.5 in the severe distortion conditions), while average ratings of local motion increased with distortion (from 1.8 in the undistorted condition to 3.3 in the moderate and 4.7 in the severe distortion conditions).

Discussion

By modulating the distortion in the stimulus, we have shown that dynamic contour integration relies upon both object and motion areas but does not preferentially involve early retinotopic areas. The observed changes in neural activity likely reflected the changing global percept and not the physical stimulus as encoded by early visual cortex.

Distortion Modulation in Slit-Viewing Conditions

The overall pattern of cortical activity in MT+ and LOC is similar for the three slit conditions, with both areas

showing the greatest activity when integration was possible and the least activity when integration was disrupted. In early retinotopic areas, activity did not differ for the three slit-viewed conditions, which suggests that the activity of higher visual areas reflects computations beyond early encodings of the physical characteristics of the stimulus.

The LOC has been shown to be sensitive to object shape in numerous prior studies [6–8]. Its activity here is likely to represent the output of the computation that integrates shape from dynamic displays, though the LOC could also play an integral role in the computation itself. The activity in the LOC was lower for slit-viewed than for fully visible objects. This may reflect a weaker representation of object shape when information must be integrated over time that was not reflected in subjects' near-ceiling behavioral performance. It is possible that a more sensitive behavioral test would confirm subjective reports that undistorted slit-viewed stimuli produce weaker perception of shape than do fully visible stimuli.

Several different explanations exist for the pattern of activity observed in MT+. One possibility is that it reflected subjects' ability to perceive global motion. AI-

though stimulus motion was present in all the slit-view conditions, coherent global motion was disrupted by the distortion. While most neurons in V1 and some in MT respond only to the local components of motion, a large number of neurons in MT have been found that represent global motion [11, 12]. Such neurons would likely show less signal when global motion signals are obscured by our “V” distortion, producing the pattern of results observed here. However, it is also known that neurons in MT participate actively in the computation of structure from motion [13]. This raises the possibility that the increases in activity we observed in MT+ reflected the computation of object structure in the slit-viewing paradigm. The current data cannot determine whether the additional activity in MT in the undistorted slit and fully visible conditions was due to global motion recovery, shape recovery, or both. Finally, it remains a possibility that activity in area MT decreased simply due to the loss of low spatial frequency information produced by the distortion process. This seems unlikely, however, since activity trends downward even for the moderate distortion, which did not greatly attenuate low spatial frequencies in the stimulus.

Shape and Motion Recovery in Slit Viewing

Area MT+ showed only a small, nonreliable difference between the fully visible and nondistorted slit-view conditions, while the LOC showed a larger, reliable difference. This pattern of results suggests that the global motion was more strongly represented than the object shape in the undistorted slit-view condition. Indeed, if the strength of area MT+ activation is taken as a measure of motion representation, the undistorted slit-view condition produced a representation that was almost as strong as that produced by the fully visible motion.

This difference between regions must be interpreted with great caution, however. First, as noted above, some of the activity in MT+ during the slit-view conditions may be attributable to computation of object structure. In addition, it is possible that, because MT overrepresents the foveal area, the slit stimulus within the fovea activates most of the MT cells that are also activated in the fully visible condition. Both of these factors could mask a difference in the strength of motion representation between the slit-view and fully visible condition.

In contrast, activity in the object areas more definitely suggests that the shape of the object is better represented in the fully-visible condition than in the undistorted slit view. To reach this conclusion, however, we had to rule out the possibility that this higher fully visible activity was an artifact of the way we selected voxels for analysis. The analyses we have been using throughout these studies localized voxels in the object areas if they showed a greater response to fully visible moving objects compared with a blank mean field (see the Experimental Procedures). This localizer, however, was of course biased toward finding voxels that were active during the fully visible condition. To test whether pixel selection bias could account for our results, we selected pixels using the response of the undistorted slit-view condition. This reversed the bias toward finding voxels active in that condition. Nevertheless, the selected vox-

els still showed greater activity to the fully visible stimulus. The most likely explanation for this finding is that shape information in the slit-viewed condition was not fully recovered. The shape may have been slightly weaker or degraded, and it is known that slit-viewed objects are perceived as compressed along the direction of motion [3].

Lateralization

The lateralization of MT+ activity to the left hemisphere for the slit-viewed stimuli is most likely because the stimuli were presented to the right visual field. Cortical cells in MT are known to be lateralized, but their receptive fields do extend a little bit beyond the vertical meridian. Cells in MST are known to be more strongly bilateral from both physiological and fMRI studies [14]. It is highly likely that our ROIs included most of MT, which would account for the greater activity in the left hemisphere, but also some of area MST, which would account for the presence of bilateral activity. The greater activity for the left hemisphere LOC than for the right hemisphere LOC also most likely reflects some amount of lateralization of receptive fields.

Conclusions

The slit-viewing task poses an interesting challenge to current conceptualizations of how information is integrated between the dorsal and ventral information processing streams in the cortex [15]. Both motion and shape information need to be recovered from fragmented stimuli, and our study has provided evidence that MT+ and LOC play important roles in this computation. The possible role of MT+ in computing structure from motion might suggest a serial model in which its output is transmitted to the LOC for shape recognition. However, we warn against a strict hierarchical explanation of how these two types of information are integrated, particularly given recent findings of interactions between form and motion in the cortex. One recent report found that the loci of form and motion areas may lie adjacent to each other along both the ventral and dorsal pathways [16], while another found that MT+ may show some sensitivity to object form [17]. How extrastriate areas coordinate their activities in dynamic shape integration remains a question for future study.

Experimental Procedures

Participants

Three women and five men, ages 24–44, participated as volunteers in the study. Five of these observers were naive as to the purpose of the experiment. All observers had normal or corrected-to-normal vision.

Slit-Viewed Conditions

Stimuli

We used 150 black and white line drawings of common objects [18] that subtended approximately 3°–4° of visual angle when fully visible. The aperture consisted of a simulated gray occluding surface with a white strip in the center acting as the slit. The fixation point, a small white disk, was placed to the left of the slit so it would not be masked by motion within the slit. The object translated behind the occluder at 3.8°/s with only a narrow slice (subtending 0.12° × 3° of visual angle) visible at any time through the slit. The entire display subtended approximately 12° of visual angle. The dynamic

distortion applied to the stimuli is described above as well as in the legend to Figure 1.

Scanner Protocol and Design

Each scan consisted of six cycles, each containing a 20 s mean gray field (with fixation) followed by a 20 s block of stimuli. The stimulus condition did not vary within each 20-s block. Across the four scans that we ran, observers saw each condition six times, with each condition pseudorandomized so that it appeared no more than twice within a scan and was separated by at least one cycle of another condition. Each block contained seven objects, with each object appearing for approximately 2.8 s, moving back and forth. For each scan, the stimuli were randomly selected from our stimulus pool, without replacement.

Procedure

Observers fixated upon the white disk during the task. In order to control for attentional effort across stimulus conditions, observers also engaged in a behavioral task. Observers were asked to report via a key press whether a red dot in the stimulus appeared above or below the fixation point. The red dot subtended 0.12° of visual angle and moved along with the stimulus, appearing for 120 ms through the slit.

Motion Localizer

The motion localizer scan consisted of six cycles of a 20 s mean gray field (with fixation) followed by a 20 s presentation of low-contrast concentric annuli that expanded at a rate of $3.8^\circ/\text{s}$. The annuli subtended approximately 12° of visual angle.

Retinotopic Mapping

Retinotopic mapping was performed with standard techniques in which subjects view a rotating checkerboard pattern that encodes the polar angle in the visual field as a phase of the fMRI response [19–21].

fMRI Sequence

The observer was positioned within the scanner with a bite bar to minimize head movements. The stimulus displays were rear projected onto a screen in the scanner room with a video projector and were then viewed with a mirror.

Twelve slices were imaged every 2.5 s, taken perpendicular to the calcarine sulcus (3T; BOLD contrast; TE, 45 ms; flip angle, 80°). Each pixel was 3.125×3.125 , with a slice thickness of 4 mm and a gap of 1 mm.

Localizers

Lateral Occipital Regions

Object areas (see Figure 6) were functionally defined as those areas showing a higher cortical response to the fully visible condition relative to the mean blank field [22]. The reliability of the stimulus-driven activity was computed using the general linear model. Sinusoids were fit to each cycle of the fMRI time series to measure the amplitude of the cortical response at each pixel. Prior to fitting, the mean of each cycle was computed, and the cycle time course was converted to the percent change relative to this baseline. T-tests performed on the amplitudes between the fully visible and blank field were computed for each subject at each pixel to generate a difference map. The regions of interest (ROIs) were first selected by using combined anatomical and functional landmarks until LO was defined as voxels on the fusiform and lingual gyri that showed no systematic retinotopic organization (Figures 6C and 6D) but were above threshold in the fully visible difference map. Threshold was set at a T value of 4.0, but variations in threshold did not affect the overall pattern of results.

MT+

Motion areas were localized with a correlation map that fit a sinusoidal hemodynamic response to the alternating cycles of expanding annuli and fixation. For each voxel, a correlation coefficient was calculated across the entire MT reference scan. ROIs were defined as voxels in the lateral portions of the occipital lobe that were above threshold in the correlation map (Figure 6E). Threshold was set at a correlation coefficient of 0.3, but variations in threshold did not affect the overall pattern of results.

Retinotopic Mapping

To select early visual areas active during the slit-viewing task, a difference map was created comparing moderately distorted slit-view activity to a blank interval. This allowed us to select the relevant retinotopic region without biasing the selection of voxels toward any of the other stimuli. Regions were taken from areas near the calcarine sulcus that showed retinotopic organization in the left hemisphere (because the stimulus was always projected to right visual field) and most likely was restricted to V1/V2. (The other hemisphere was weakly active in three out of eight subjects and likely reflects bilateral V2. There were no differences in the patterns of activations in early visual cortex between hemispheres.) ROIs were defined as voxels in these retinotopic regions that were above threshold in the moderate-distortion difference map (Figures 6C and 6D). Because activity in these regions was low during slit viewing, a relatively low threshold of $T = 2.0$ was used, but, again, the pattern of results did not depend upon this choice.

Slit-Viewing Conditions

Within each ROI, we fit a sinusoid to the average cycle for each condition and each subject. The amplitudes of these sinusoids corresponded to the cortical activity of each condition and were compared with an analysis of variance (ANOVA).

Behavioral Experiment

Four of the participants in the fMRI experiment were asked to rate the perceived strength of horizontal motion and of vertical motion for seven objects shown in the undistorted, moderately distorted, and strongly distorted conditions. All objects were from the same pool as that used in the fMRI experiment. Objects were selected that were round in shape in order to eliminate biases in perceived motion direction due to the aperture problem. However, informal observations indicate that similar results would be obtained for the full object set. Stimuli were shown outside the scanner, but under similar viewing conditions to those used in the fMRI experiment. Subjects rated the strengths of motion on a 5-point scale following each stimulus presentation. Subjects also performed a naming task. Observers were first shown the objects with their names to familiarize them with the stimuli. They then viewed each object in each condition. Following each stimulus presentation, subjects typed their naming response.

Eye Movements

In order to confirm that observers were able to maintain fixation during the slit-viewing task, two observers (CY and SS) were tested outside of the scanner while using an ober2 Eye Trace System eye tracker (Permobil). These observers performed the identical dot localization task while viewing the same three types of 20-s slit-viewing sequences as used during scanning. The observers' saccades were first calibrated to obtain baseline saccade patterns to eccentricities of 1° , 3° , and 6° of visual angle from central fixation. The calibration results ensured that an eye movement at or above 1° of amplitude could easily be detected in this technique. Inspecting the results from the eye tracker revealed not a single deviation greater than the calibrated amplitude of a 1° saccade. Both observers maintained steady fixation during each of the 20-s slit-viewing conditions.

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