Perceptual Organization of Local Elements into Global Shapes in the Human Visual Cortex

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Summary

The question of how local image features on the retina are integrated into perceived global shapes is central to our understanding of human visual perception. Psychophysical investigations have suggested that the emergence of a coherent visual percept, or a "good-Gestalt" [1], is mediated by the perceptual organization of local features based on their similarity. However, the neural mechanisms that mediate unified shape perception in the human brain remain largely unknown. Using human fMRI, we demonstrate that not only higher occipitotemporal but also early retinotopic areas are involved in the perceptual organization and detection of global shapes. Specifically, these areas showed stronger fMRI responses to global contours consisting of collinear elements than to patterns of randomly oriented local elements. More importantly, decreased detection performance and fMRI activations were observed when misalignment of the contour elements disturbed the perceptual coherence of the contours. However, grouping of the misaligned contour elements by disparity resulted in increased performance and fMRI activations, suggesting that similar neural mechanisms may underlie grouping of local elements to global shapes by different visual features (orientation or disparity). Thus, these findings provide novel evidence for the role of both early feature integration processes and higher stages of visual analysis in coherent visual perception.

Results and Discussion

Traditional approaches of visual processing [2] suggest that the analysis of local image features involves early visual areas (i.e., striate and extrastriate retinotopic regions), while higher visual areas (i.e., regions in the inferotemporal cortex) mediate the perception and recognition of global shapes. However, the neural substrates of the perceptual organization of local features into global shapes in the human brain remain largely unknown.

By combining psychophysical and human event-related functional magnetic resonance imaging (fMRI) techniques, we demonstrate that not only higher occipitotemporal but also early retinotopic areas are involved in the perceptual organization and detection of global shapes. Specifically, we tested for responses to global shapes in early retinotopic ventral areas (V1, V2, Vp, and V4v) and

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the human lateral occipital complex (LOC), a region in the lateral occipital cortex that extends anteriorly into the temporal cortex and is thought to be involved in the analysis of the perceived object shape [3–6] and processes of object recognition [7, 8] (Figure 1). We employed closed contours rendered by similarly oriented local elements and embedded in a background of randomly oriented elements. Such displays yield the perception of a global figure in a randomly textured background (Figure 2) and are thought to emerge from a segmentation process that relies on the integration of the similarly oriented elements into global configurations [9, 10].

The goal of Experiment 1 was to test responses to global contours versus random patterns across visual areas. To this end, we presented the subjects with Collinear Contours consisting of a closed contour of similarly oriented Gabor elements embedded in a background of randomly oriented Gabors, Stereo and Collinear Contours that consisted of collinear contours presented stereoscopically in front of the background elements, and random versions of these displays that consisted of a field of randomly oriented elements (Random Patterns and Stereo Random Patterns). The subjects' accuracy was high in discriminating global contours from random patterns. In particular, detection accuracy was high for Collinear Contours (d-prime: 2.19, 82.3% hits and 89.5% correct rejections for the Random Patterns) and Stereo and Collinear Contours (d-prime: 2.82, 92.7% hits and 91.1% correct rejections for the Stereo Random Patterns).

Analysis of the fMRI responses showed stronger responses for collinear (Collinear Contours and Stereo and Collinear Contours) than for random patterns (Random Patterns and Stereo Random Patterns) in all the early ventral visual areas (V1, V2, VP, and V4v) and the LOC (Figure 3A). A repeated measures ANOVA on the peak responses across all regions of interest (ROIs) showed significant effects for Image Type (Contour, Random Pattern) (F[1, 36] = 17.31, p < 0.01), but not for ROI (F[4, 36] < 1, p = 1.00) or Grouping Cue (Collinearity, Stereo and Collinearity) (F[1, 36] < 1, p = 0.57). No significant interaction was observed between ROI and Image Type (F[4, 36] < 1, p = 0.67). These findings suggest that both early and higher visual areas respond more strongly to global contours than to random patterns when their components (Gabor elements) are grouped by collinearity or by additional disparity information.

Interestingly, as shown in Figure 3B, we observed stronger responses in the LOC when additional disparity information was used for grouping the contour elements. A significant interaction between ROI and Grouping Cue was observed (F[4,36] = 3.48, p < 0.05). Contrast analysis showed significantly stronger responses for the Stereo and Collinear Contours than the Collinear Contours condition in the LOC (F[1,36] = 5.62, p < 0.05), but not in early visual areas. Consistently, analysis of the behavioral data showed a facilitative trend when
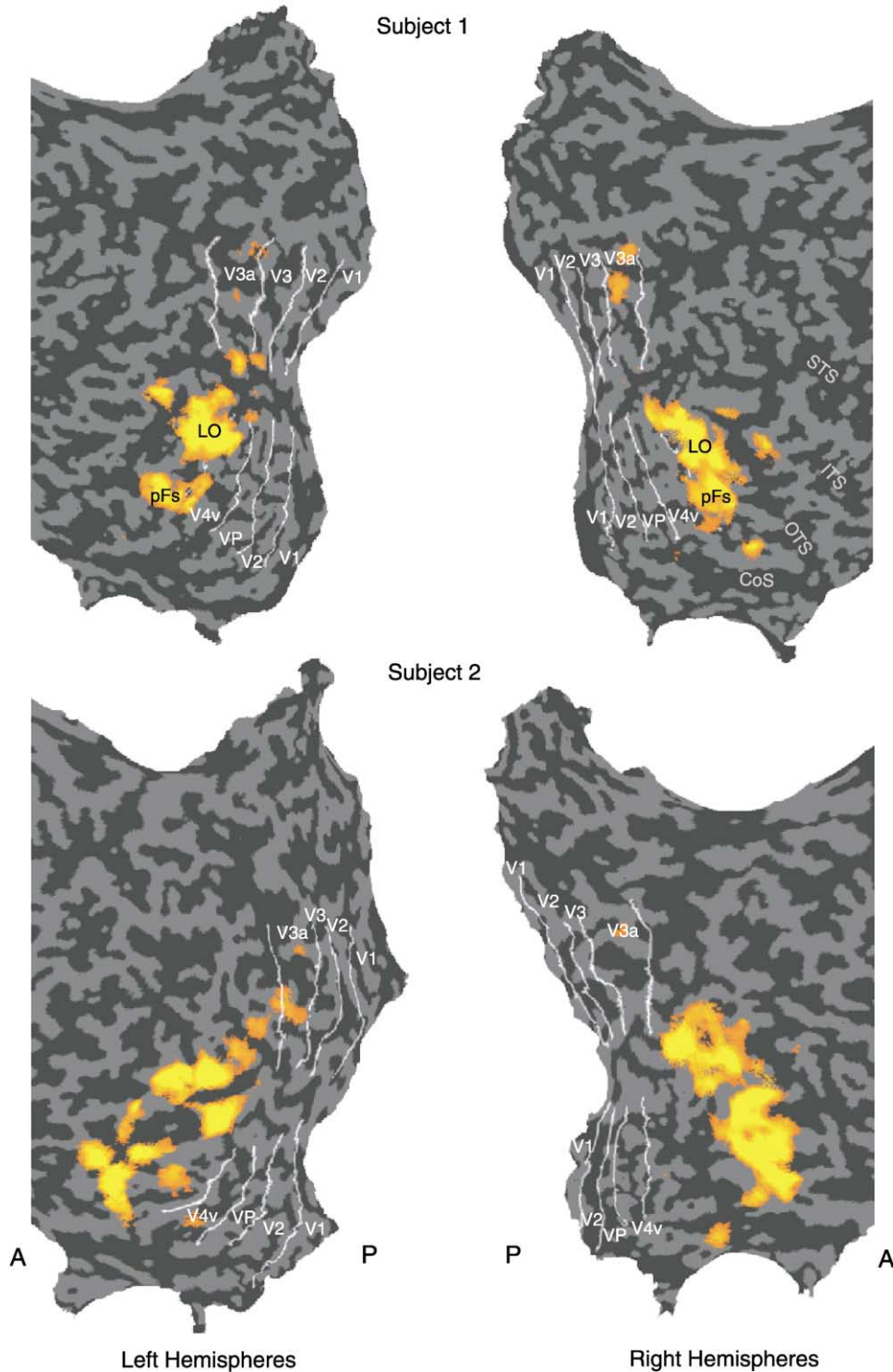
Figure 1. Functional Localization of ROIs

Functional activation maps for two subjects showing the early retinotopic regions and the LOC. The functional activations are superimposed on flattened cortical surfaces of the left and right hemispheres. The sulci are coded in darker gray than the gyri, and the anterior-posterior orientation is noted by A and P. Major sulci are labeled: STS, superior temporal sulcus; ITS, inferior temporal sulcus; OTS, occipitotemporal sulcus; CoS, collateral sulcus. The borders (shown by lines) of the early visual regions (V1, V2, VP, V3, V3a, and V4v) were defined with standard retinotopic techniques. The LOC was defined as the set of all contiguous voxels in the ventral occipitotemporal cortex that were activated more strongly ($p < 10^{-4}$) by intact than by scrambled images of objects. The posterior (lateral occipital [LO]) and anterior (posterior fusiform [pFs]) regions of the LOC were identified on the functional maps based on anatomical criteria, as described previously [7].

A Collinear Contour

B Misaligned Contour
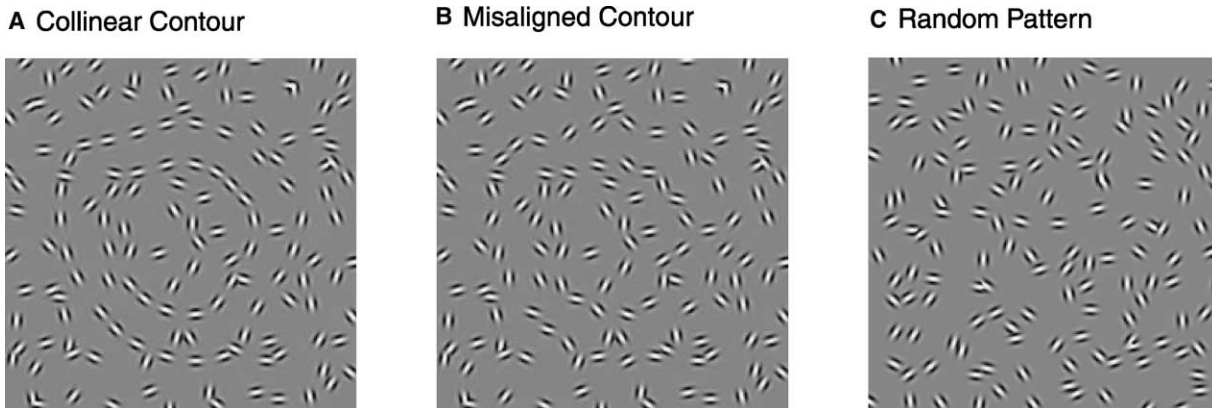
C Random Pattern

Figure 2. Stimuli

(A–C) An example of the stimuli used in Experiments 1 and 2: (A) Collinear Contours, (B) Misaligned Contours, and (C) Random Patterns.

disparity information was added to collinear contours (F[1, 9] = 4.56, p = 0.06). However, this effect of Grouping Cue (Collinearity, Stereo and Collinearity) was only marginally significant, possibly due to the ceiling performance levels at the Collinear Contours condition. These results suggest that, while collinearity is a strong cue for contour integration, additional information (i.e., disparity) that facilitates grouping and enhances the saliency of the global shape may modulate responses in the LOC consistent with its known involvement in the processing of the perceived global shape.

In Experiment 2, we investigated further the role of the different visual areas in the detection of global contours that differed in their perceptual coherence by manipulating the alignment of the local contour elements. We tested the subjects' detection performance on Collinear Contours, as described in Experiment 1, and Misaligned Contours, which were generated by rotating the collinear elements randomly within a range of ±25–30°C. We also tested the effect of grouping by disparity on the detection of contours when their local elements were misaligned (Stereo Misaligned Contours). Detection accuracy was significantly higher (F[2, 16] = 13.04, p < 0.001) for Collinear (d-prime: 1.97, hits: 86.0%) and Stereo Misaligned Contours (d-prime: 1.68, hits: 78.7%) than for Misaligned Contours (d-prime: 0.77, hits: 46.2%). These results suggest that decreased detection performance for misaligned contours was improved by grouping based on disparity, consistent with previous psychophysical studies providing evidence for the role of depth information in contour integration [11, 12] and surface perception [13].

Analysis of the fMRI data showed that the responses in both early and higher visual areas were modulated in correspondence to the subjects' detection performance. As shown in Figure 4, fMRI responses for detected Contours (Collinear Contours, Stereo Misaligned Contours, Detected Misaligned Contours: trials in which the subjects responded correctly) were significantly stronger (F[1,48] = 7.07, p < 0.05) than for Nondetected Contours (Nondetected Misaligned Contours: incorrect trials) across visual areas (Figure 4). No significant interaction (F[6,48] = 1.77, p = 0.12) was observed between ROI

and Condition, suggesting that the fMRI responses were similar across visual areas.

The findings of this study demonstrate that the perceptual organization of local elements into global shapes involves not only higher occipitotemporal areas that have traditionally been thought to be the main neuronal locus of shape perception, but also early retinotopic regions. We found that both early and higher visual areas show stronger responses to contours defined by local elements grouped by orientation and/or disparity than to randomly oriented local elements. More importantly, when the global structure of the shapes was disturbed by misalignment of the local contour elements, the detection performance of the subjects and the fMRI activations decreased. In contrast, grouping of misaligned contour elements by additional cues (i.e., disparity) increased the performance of the subjects and the fMRI activations, suggesting that similar neural mechanisms may underlie grouping of local elements to global shapes by different visual features (orientation or disparity).

One possible limitation of our experiments is that the observed fMRI responses could be modulated by differences in the subjects' attention at different stimulus conditions. However, analysis of the behavioral results of the subjects in the scanner for Experiment 1 showed no significant differences in the reaction times of the subjects for contours (736 ms) and random patterns (733 ms) (F[1, 9] < 1, p = 0.88). In Experiment 2, the subjects were significantly (t[8] = 4.03, p < 0.01) slower in responding to nondetected misaligned contours (992 ms) than to detected ones (794 ms). These results indicate that the subjects did not simply ignore the random or misaligned patterns, but they responded faster when they detected a contour than when not. Furthermore, we observed similar fMRI activations in six additional subjects that were presented with contours and random patterns outside their attentional focus while performing a dimming task (i.e., detection of luminance changes on the fixation point). Thus, stronger fMRI responses to collinear than to random patterns indicate neural mechanisms responsive to the global contours rather than attentional modulation effects across conditions.
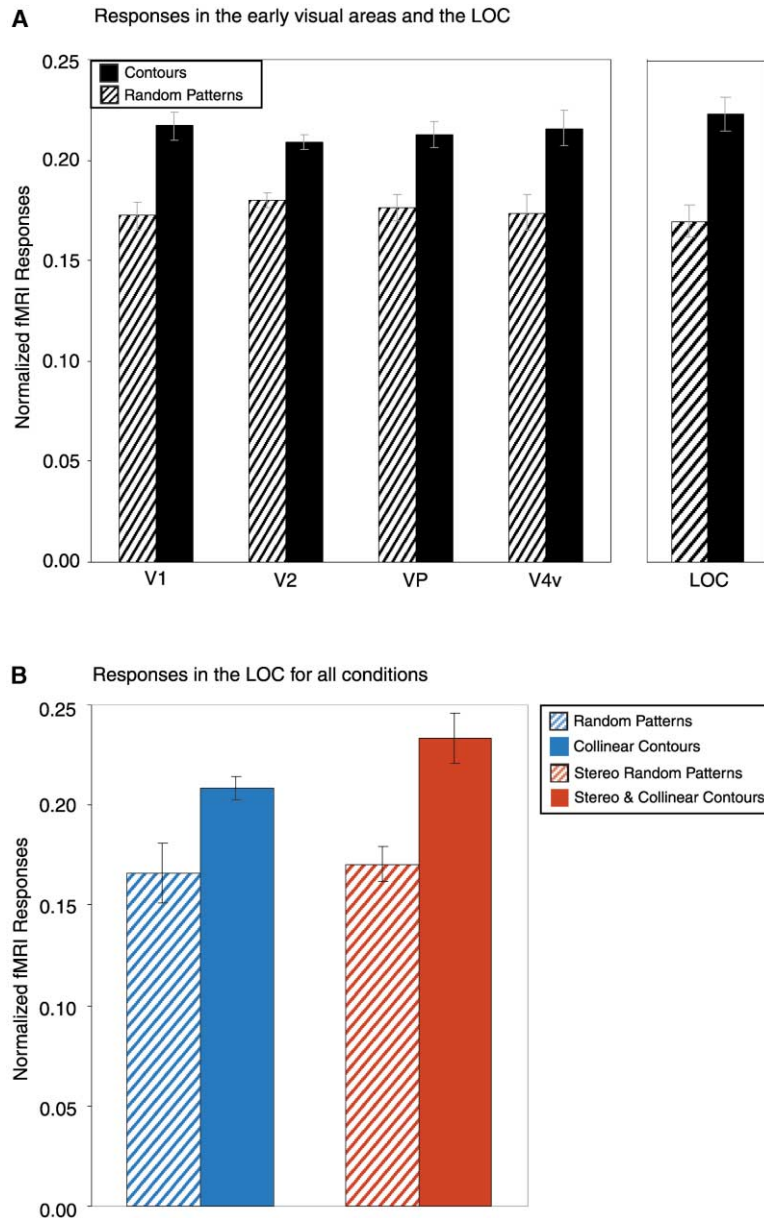
A Responses in the early visual areas and the LOC

Figure 3. Results for Experiment 1

(A) fMRI responses for contours (average responses for Collinear Contours and Stereo and Collinear Contours) versus random patterns (average responses for Random Patterns and Stereo Random Patterns) across early ventral visual areas and the LOC.

(B) fMRI responses in the LOC for all stimulus conditions. We plot normalized fMRI responses that were calculated individually for each subject by subtracting the mean percent signal change for all of the conditions within each ROI from the mean percent signal change for each condition and then adding the mean percent signal change for all the conditions across subjects and ROIs. These normalized fMRI responses at the peak time points (3–5 s after stimulus onset) indicate differences across conditions independent of the variability in the fMRI signal across subjects, ROIs, and scanning sessions. The error bars indicate mean standard errors on the fMRI responses for each condition averaged across trials (28 per scan), scans (4), and subjects (10). Additional analysis in posterior (LO) and anterior (pFs) subregions of the LOC showed similar patterns of results; that is, we observed stronger fMRI responses for contour stimuli versus random patterns ($F[1, 9] = 22.52$, $p < 0.001$) in these subregions and no significant difference between the two subregions ($F[1, 9] < 1$, $p = 0.50$).

B Responses in the LOC for all conditions

Our findings are consistent with several neurophysiological studies that suggest that recurrent mechanisms of visual processing, based on local connections or feedback interactions, mediate global processing (for reviews, see [14–19]). Long-range connections [15, 16, 20, 21] are suggested to link neurons of similar orientation tuning across large distances within V1 and result in modulation of the responses to oriented stimuli inside the receptive field (RF) of V1 neurons by contextual stimuli outside the RF [20–25]. Consistently, several studies have shown that figure-ground segmentation [17, 18, 26–29] and figure-border assignment processes in areas V1 and V2 [30, 31] mediate the segmentation of target elements from their background and facilitate the successful integration of global configurations. Responses to global configurations in early visual areas may then be forwarded to higher visual areas (i.e., V4, occipito-temporal regions) that are known to have larger RFs, process complex feature configurations [32–34], represent the perceived visual shape rather than the local contours [6, 35], and mediate processes of object recognition [7, 8, 36, 37].

Alternatively, feedback connections [17, 18, 27, 28, 38, 39] from higher visual areas may modulate processing in early visual areas. Specifically, increased responses are observed in V1 neurons at longer latencies when the RF is on the figure rather than the background of the stimulus [17, 18, 27, 28, 39]. These temporal differences in the contextual modulation effects suggest that feedback from higher visual areas may mediate figure-ground perception.

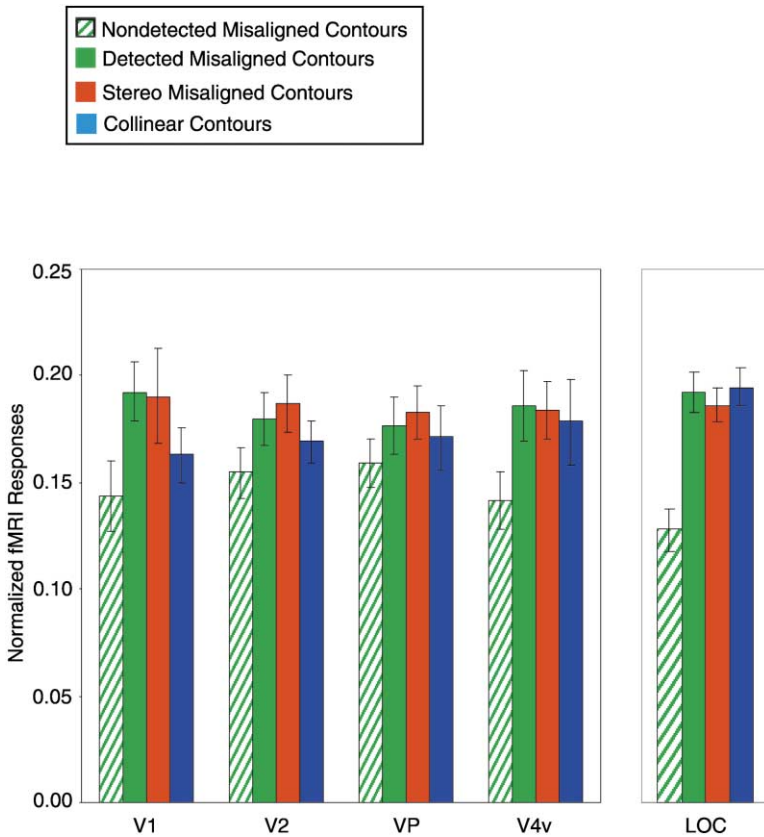Consistent with this top-down interpretation, we ob-

Figure 4. Results for Experiment 2

fMRI responses for the Nondetected Misaligned Contours, Detected Misaligned Contours, Stereo Misaligned Contours, and Collinear Contours conditions for the early visual areas and the LOC. We plot normalized fMRI responses, as described in Figure 3, and mean standard errors on the normalized percent signal change for each condition averaged across trials (16 per scan), scans (4), and subjects (9). Responses to detected contours (Detected Misaligned Contours, Stereo Misaligned Contours, and Collinear Contours) were significantly stronger than responses to nondetected contours (Nondetected Misaligned Contours) in V1, V4v, and the LOC. Additional analysis in posterior (LO) and anterior (pFs) subregions of the LOC showed significantly stronger fMRI responses for detected than nondetected contours ($F[1, 24] = 5.44$, $p < 0.01$) in these subregions and no significant difference between the two subregions ($F[1, 24] = 2.75$, $p = 0.13$).

served stronger activations in the LOC, but not in the early visual areas, for collinear than for misaligned patterns when the subjects performed a two alternative-forced choice (2AFC) task (see Figure S1 in the Supplementary Material available with this article online). The similarity of the LOC results across tasks (detection, 2AFC) provides additional evidence that our findings could not be due to differences in the task demands or the general state of attention across conditions. However, the pattern of results observed in the early visual areas suggests that the presence/absence decision required by the subjects in the contour detection, but not in the 2AFC, discrimination task may modulate the fMRI responses in the early visual areas. That is, the responses in early visual areas are enhanced when a contour is detected but suppressed when not. These results are consistent with several studies showing task-dependent modulation of activity in early visual areas (e.g., [40–42]) that are related to increases in the signal-to-noise ratio due to differences in the attentional demands across tasks. For example, it is possible that attention to the target contours was enhanced after detection and contributed to the increased responses to collinear contours in V1. Finally, consistent with recent studies showing that the hemodynamic responses reflect the synaptic input and processing in an area rather than the output [43], our findings suggest that the responses to global contours in early visual areas may be the result of top-down modulation by higher occipitotemporal areas (i.e., LOC). Further studies are required to distinguish

between the role of local interactions and feedback connections in global shape perception.

In summary, our study demonstrates that both early and higher stages of visual analysis are involved in global shape perception. These findings advance our understanding of the neural basis of coherent visual perception in several aspects. First, previous neurophysiological studies have suggested that recurrent visual processing may underlie perceptual phenomena, such as the pop-out of targets [20, 23, 44–50], the perception of surfaces [51, 52], and the detection of collinear paths [53, 54]. By combining behavioral and fMRI methods, our study provides novel evidence that similar processes in the human brain may mediate the detection of coherent contours that are shown to be perceived as global shapes rather than simple targets, surfaces, or paths [9, 10]. Second, our findings suggest that similar mechanisms underlie this integration process of local elements to global shapes by different visual features (e.g., orientation, disparity). Finally, conventional methods have characterized different brain regions based on their preferable tuning to stimuli that differ in their low-level features (e.g., single oriented lines or textured targets for early visual areas versus complex objects for high visual areas). In contrast, our study makes use of an alternative approach that manipulates the global coherency of the same stimulus to investigate the involvement of various cortical areas in perception. Thus, the present study is a first step in understanding the functional connectivity across visual areas in the

human brain that underlie the awareness of coherent visual percepts.

Experimental Procedures

Subjects
Twenty students, ten in each experiment, from the University of Tübingen participated in this study. The data from one subject in Experiment 2 were excluded due to excessive head movement.

Materials
We used random and collinear stimuli rendered with Gabor elements (oriented sinusoidal luminance features [3.8 cycles per degree of visual angle] with Gaussian envelopes that roughly model the RF structure of V1 simple cells) as described in previous studies [9, 10, 55, 56]. The Collinear Contours consisted of two concentric, closed shapes that covered an average area of $6° \times 6°$ and were embedded in a rectangular field ($10.9° \times 10.9°$) of randomly oriented background Gabor elements. For all the stimuli, the size of the Gabor elements was $0.5°$, and the distance between them was $0.5°$. We used 70 different closed shapes for the collinear patterns. The Random Patterns consisted of a rectangular area ($10.9° \times 10.9°$) filled with randomly oriented Gabor elements. The Stereo and Collinear Contours consisted of collinear contours that were presented stereoscopically ($0.14°$ disparity) in front of the background Gabor elements. The Stereo Random Patterns consisted of random patterns with a number of randomly oriented elements presented in the front plane ($0.14°$ disparity). These stereoscopically presented random elements were of the same number and covered approximately the same area as the collinear elements in the Stereo and Collinear Contours. All the stereoscopic stimuli were rendered as red-green anaglyphs, and the depth arrangement of the stimuli was perceived via the use of red-green glasses.

Procedure
Each subject participated in a single session for only one of the experiments. Each experiment consisted of eight scans: two LOC localizer scans, two localizer scans for the early retinotopic areas, and four event-related scans for the experiment. The order of the scans was counterbalanced across subjects.

The event-related scans consisted of one epoch of experimental trials and two 8-s fixation epochs, one at the beginning and one at the end of the scan. For Experiment 1, each scan consisted of 14 experimental trials for each of the 4 conditions and 14 fixation trials. For Experiment 2, each scan consisted of 16 experimental trials for each of the Collinear Contours, Misaligned Contours, and Stereo and Misaligned Contours conditions, 8 catch trials for each of the Random Patterns and Stereo Random Patterns conditions, and 16 fixation trials. A new trial began every 3 s and consisted of a stimulus image presented for 300 ms and a blank interval of 2700 ms. As in previous studies [5, 6], the order of presentation was counterbalanced so that trials from each condition, including the fixation condition, were preceded (2 trials back) equally often by trials from each of the other conditions. Different stimuli were presented across conditions, but all the stimuli were presented in all conditions across subjects. For both experiments, the subjects performed a contour detection task; that is, they indicated via button presses whether they detected a global shape (consisting of two concentric closed contours) or not.

Imaging
For all of the experiments, scanning was done on the 1.5 T Siemens scanner at the University Clinic in Tübingen, Germany. A Gradient Echo pulse sequence (TR = 2 s, TE = 90 ms for the localizer scans; TR = 1 s, TE = 40 ms for the event-related scans) was used. Eleven axial slices (5 mm thick with 3.00×3.00 mm in-plane resolution) were collected with a head coil.

Data Analysis
fMRI data were processed with the BrainVoyager 4.6 software package. For each individual subject, the regions of interest (ROIs) defined were the LOC (Talairach coordinates: mean for right hemispheres: 39.1, −65.6, −12.0; mean for the left hemispheres: −41.9, −64.8,

−2.7) and the retinotopic ventral areas (V1, V2, VP, and V4v). For each individual subject, the LOC was defined as the set of continuous voxels in the ventral occipitotemporal cortex that showed significantly stronger activation ($p < 10^{-4}$) to intact than to scrambled images of novel and familiar objects, as described previously [5]. The early visual areas were identified based on standard retinotopic mapping procedures [7, 57–60].

For each event-related scan, the fMRI response was extracted by averaging the data from all the voxels within each one of these independently defined ROIs based on the hemodynamic response properties [61–63] and as described in previous studies [5, 6]. Specifically, we averaged the signal across trials in each condition at each of the 11 corresponding time points (seconds), converted these time courses to percent signal change relative to the fixation trials, and averaged the time courses for each condition across scans and subjects. ANOVAs on the average percent signal change from these 11 time points were conducted across stimulus conditions and subjects in each one of the predefined ROIs. These ANOVAs showed significant interactions (e.g., Experiment 1: V1: $F[30, 270] = 1.97$, $p < 0.01$; LOC: $F[30, 270] = 3.00$, $p < 0.001$) between conditions (Collinear Contours, Random Patterns, Stereo and Collinear Contours, Stereo Random Patterns) and time (11 time points). Contrast analysis showed significant differences between conditions for time points 3, 4, and 5 (e.g., Experiment 1: V1: $F[30, 270] = 73.02$, $p < 0.001$; LOC: $F[30, 270] = 120.90$, $p < 0.001$), but not for the onset of a trial, i.e., time point 0 (e.g., Experiment 1: V1: $F[30, 270] = 1.11$, $p = 0.29$; LOC: $F[30, 270] < 1$, $p = 0.36$). Similar effects were observed across visual areas and experiments. Thus, these three time points were selected as the peak of the event-related responses.

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