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# Magnetic responses of human visual cortex to illusory contours

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## Abstract

To examine the neural mechanism underlying illusory-contour perception, we measured the magnetic responses of the human visual cortex to an abutting-line grating inducing illusory contours (test stimulus) and a non-abutting-line grating (control stimulus) using the technique of magnetoencephalography (MEG). In the initial latency period of 60–80 ms, the MEG response to the test stimulus was nearly identical with that to the control stimulus, but in the subsequent period of 80–150 ms, the former was larger than the latter. The origin of the peak MEG response to the test stimulus was estimated to be in the vicinity of striate cortex/extrastriate visual cortex for two of the four subjects. These results suggest that, in accord with those of the previous electrophysiological and functional magnetic resonance imaging studies, illusory-contour signals are generated in the very early stage(s) of processing in the primate visual cortex. © 2002 Elsevier Science Ireland Ltd. All rights reserved.

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Natural scenes are filled with objects at different distances from an observer. Since most of them are opaque rather than transparent, occlusion of objects is a ubiquitous phenomenon in our visual world. In order to 'see' such a world in a meaningful way, the visual system has not only to discriminate the boundaries of objects, but also to integrate separate fragments of an occluded object into a single unit. The existence of the integrative process in the human visual system is highlighted by the phenomena called illusory, or subjective, contours [7,13,15] or amodal completion behind an occluder [8].

To account for illusory-contour perception, traditional psychological studies have emphasized cognitive/top-down processes [3,14], but recent physiological studies have suggested that illusory-contour perception may be mediated by sensory/bottom-up processes. Single-cell studies of monkeys have shown that illusory-contour responses are obtained from neurons in the extrastriate visual cortex (V2) [12,17,18], and also from as early as those in the striate cortex (V1) [4]. On the other hand, human functional magnetic resonance imaging (fMRI) studies have shown that illusory-contour stimuli activate multiple cortical areas, not only V1/V2 [2,6] but also those throughout the visual pathway through V3A and up to V4v/V8 [10]. Given these findings, it is important to clarify the roles of these multiple areas in generating illusory-contour perception. One useful strategy is to examine the temporal properties, as well as the amplitude, of the cortical activities, thereby elucidating the temporal flow of the illusory-contour signals in the visual pathway. In the present study, we recorded magnetic responses of the human visual cortex to illusory-contour and non-illusory-contour stimuli using magnetoencephalography (MEG) which has high (millisecond-order) temporal resolution. The results have previously been published in abstract form [11].

Four healthy volunteers (all males, aged 22–44 years) served as subjects. All subjects gave informed consent prior to participation in this study. They had normal or corrected-to-normal visual acuity. Visual stimuli were generated using a VSG2/3 stimulus generator (Cambridge Research Systems, Rochester, UK) and displayed on a CRT monitor placed outside a magnetically-shielded room. The stimulus display (24.7° (W) by 18.7° (H)) was viewed binocularly at a viewing distance of 800 cm through a custom-

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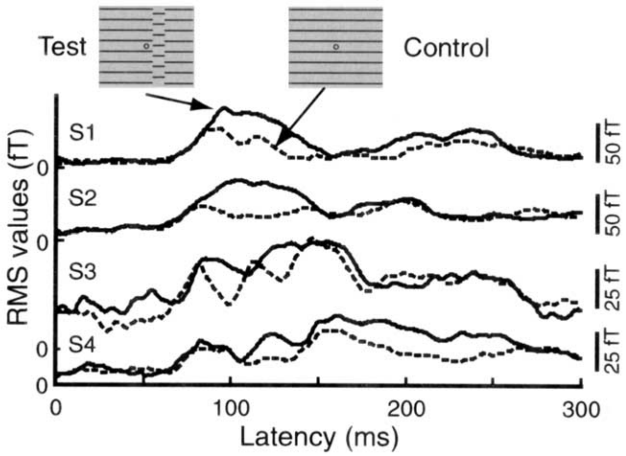

Fig. 1. Averaged MEG responses for the four subjects as a function of time from the stimulus onset. In each of the four sets of data, the solid and the broken waveforms indicate the RMS values for the test and control stimuli, respectively. For S1 and S2, the RMS values show that the initial rising portions (in the latency period of 60–80 ms) of the MEG responses to the test and control stimuli are almost identical, but in the subsequent portion (80–150 ms), the MEG response to the test is larger than that to the control. These tendencies are observed also for the other subjects (S3 and S4), although the difference is smaller (see the scale bars), and the difference for S4 is observed only in the later period of 100–130 ms. Note that, for S3, the zero level of the RMS values is displaced downward for the clarity of the figure.

made optical system and a binocular telescope of 12 magnifications. The stimulus configurations are schematically illustrated in the insets of Fig. 1. The control stimulus was a line grating composed of horizontal lines (24.7° × 3.7′) with an inter-line spacing of 0.43° (see the right inset in Fig. 1). The test stimulus was an abutting-line grating made by vertically displacing (by 0.22°) the short segments of the component lines (see the left inset). With these configurations, the test stimulus induced clear illusory contours at 0.62 and 1.54° right from the center of the display, while the control did not give rise to any illusory contours. The luminance of each line was 5 cd/m$^2$, and that of the background was 35 cd/m$^2$. A fixation marker was presented continuously at the center of the display. The stimulus was presented for 500 ms, followed by the uniform background which lasted at least 1000 ms. Within each experimental session, the presentations of the test and control stimuli were randomized across trials.

Visually evoked magnetic responses were recorded with a 129-channel MEG system (SBI-100; Shimadzu Corp., Kyoto, Japan). The system consisted of 43 vector-gradiometers, each of which was composed of a triplet of axial first-order differential coils with a baseline of 50 mm. Each coil of the gradiometer was elliptical in shape with major and minor axes of 27 and 16 mm, respectively. The three coils shared a common center-point with their planes mutually intersecting at right angles. Thus, at each of the 43 measuring points, a radial and two tangential (i.e. three-dimensional) components of the magnetic fields could be calculated. The gradiometers resided in a fiberglass helium dewar and were distributed in a circular array which extended 24 cm in diameter over a concave dewar base with 25 mm spacing.

During an experimental session, the subject was seated with his head prone on a forehead rest, looking downward at a front-silvered mirror on the floor on which the stimulus display was projected. The subject's head, with four flat positioning-coils attached, was stabilized rigidly by 'sandwiching' the head between the forehead rest and the dewar centered above the occipital pole of the subject. Coil positioning measurement was conducted before the MEG measurements by passing tiny currents through the coils, and the position of the subject's head was converted to the *XYZ*-coordinates of the MEG system.

In each MEG measurement, the magnetic fields within an initial period of 100 ms before the stimulus presentation were used to calculate the noise level, and the visually evoked fields were evaluated with reference to the noise level. The evoked magnetic fields were bandpass-filtered (1 Hz analog high-pass and 100 Hz digital low-pass filtering), sampled at 1 kHz for 1024 ms, and digitized with a 16-bit resolution. For each stimulus condition, 100 (S2 and S3) or 200 (S1 and S4) trials were executed and the evoked magnetic fields were averaged over all the trials. A single equivalent current dipole (ECD) model was used to estimate the location of the cortical activities using a spherical conductor model that approximated the subject's head shape. The reliability of the calculated ECDs was evaluated with the goodness of fit (GOF; %) defined as:

$$\mathrm{GOF} = \left[1 - \sum(\mathrm{MF_m} - \mathrm{MF_c})^2 / \sum \mathrm{MF_m^2}\right] \times 100$$

where $\mathrm{MF_m}$ and $\mathrm{MF_c}$ are the measured and the calculated fields, respectively. The ECDs were accepted when the GOF exceeded 95%, and were co-registered with the magnetic resonance images of the subject's brain.

The four sets of data in Fig. 1 show the time courses of the MEG responses for the four subjects. In each set, the solid waveform indicates the root mean square (RMS) values for the test stimulus across the 43 measuring points of the averaged MEG data and the broken curve indicates those for the control stimulus. For the two subjects (S1 and S2), the initial rising portions of the MEG responses to the test and control stimuli are almost identical in the latency period of 60–80 ms from the stimulus onset. In the subsequent period of 80–150 ms, on the other hand, there is a difference between the two responses, with the response to the test being much larger than that to the control. These tendencies are observed also for the other subjects (S3 and S4), although the MEG responses and the magnitude of the difference are smaller (see the scale bars), and the difference for S4 is observed only in the later period of 100–130 ms.

The present results suggest that the initial rising portion of the MEG responses may be contributed to by cortical activities common to the test and control stimuli which are presumably related to extraction of local features of the stimuli (e.g. line segments), whereas the subsequent portion may be contributed to by activities which are related to the generation of illusory-contour signals (e.g. completion of the spatial gaps between the line terminations). To examine the cortical area(s) contributing the MEG responses to the test and control stimuli, we applied the ECD model at the peak latency of the RMS values for each subject and stimulus. For the test stimulus, reliable ECDs were obtained for the first two subjects (S1: GOF = 96.6%, latency = 96 ms; S2: 96.0%, 104 ms), but not for the other two (S3 and S4: GOF < 95%) due to the smaller response amplitudes. For S1 and S2, the ECD locations and the isocontour maps (radial components of the magnetic fields) for the test stimulus are shown in Fig. 2. In the figure, the ECDs and maps for the control stimulus are also shown for comparison, although the GOF values did not reach our criterion level (see below). For both subjects, the isocontour maps for the test stimulus show one dipole pattern consistent with the high GOF values, and the ECDs are located in the vicinity of the calcarine sulcus of the left hemisphere which is contralateral to the position of the illusory contours (i.e. right visual field). Talairach coordinates of the ECDs are (−18, −96, 7) for S1 and (−15, −83, 6) for S2, which are estimated to be within V1 or V2 [16]. On the other hand, the isocontour maps for the control stimulus show multi-dipole patterns with more than one region of out-going and in-going magnetic fields (it is especially evident for S2 and somewhat less clear for S1), resulting in the lower GOF values (S1: 92.6%, 92 ms; S2: 88.5%, 83 ms). This is likely to be due to the fact that the control stimulus was composed of the horizontal lines extending over the two (left and right) visual fields by which cortical activities may well be caused in both hemispheres. Note here that, in spite of the fact that the test stimulus was also composed of the line segments in the two visual fields, the peak MEG response to the test stimulus was well explained by the single ECD model. Thus, one may say that the response to the test stimulus was contributed to mainly by the cortical activities related to the illusory contours (in the right visual field) which were localized in one (left) hemisphere.

The present study demonstrated that, for two of the four subjects, the MEG response to the illusory-contour stimulus showed a difference from that to the control stimulus. The difference emerged in the latency period of 80–150 ms which was only 20–30 ms later than the onset of the MEG response (approximately 60 ms). The ECD locations for the test stimulus indicated that the MEG response to the illusory contours might be contributed to by the cortical activities in V1/V2. The early emergence of the difference agrees with the results of the recent monkey study which showed that population averaged responses of V1/V2 neurons to illusory contours emerged 70–100 ms after the stimulus onset [9]. The ECD locations are consistent with the results of monkey single-cell studies and human fMRI studies which showed that V1 and V2 could respond to illusory contours [2,4,5,12,17,18].

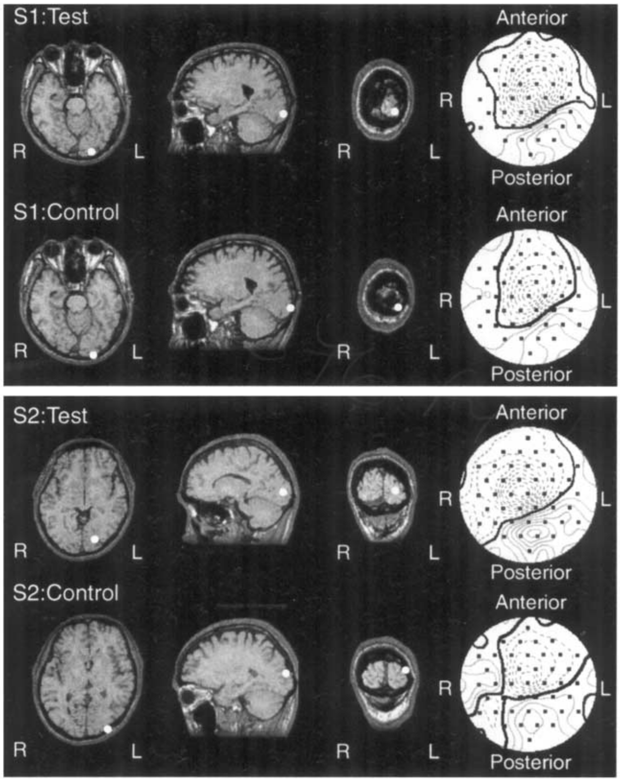

Fig. 2. ECD locations (indicated by white circles) and isocontour maps (radial components of the magnetic fields) at the peak latency of the RMS values of the MEG response to the test and control stimuli. Thick lines in the maps indicate zero magnetic field, and thin and dotted lines indicate the out-going and in-going magnetic fields, respectively. A line is drawn every 30 fT. For the test stimulus, reliable ECDs were obtained for S1 (GOF = 96.6%; latency = 96 ms) and S2 (96.0%; 104 ms) but not for the other two subjects (GOF < 95%). The isocontour maps for S1 and S2 show one dipole pattern and ECDs are located in the vicinity of the calcarine sulcus of the left hemisphere which is contralateral to the position of the illusory contours. Talairach coordinates of the ECDs are (−18, −96, 7) for S1 and (−15, −83, 6) for S2. For the control stimulus, the isocontour maps show multi-dipole patterns with more than one region of out-going and in-going magnetic fields (it is especially evident for S2 and somewhat less clear for S1), resulting in the lower GOF values (S1: 92.6%, 92 ms; S2: 88.5%, 83 ms).

On the other hand, one fMRI study has shown that illusory-contour stimuli activate not only the lower-tier areas of V1/V2, but also the higher-tier areas of V3A, V7, V4v and V8, and the activation is stronger in the latter areas [10]. The activations in the higher-tier areas were not obtained in the present study, suggesting that our stimulus configurations (and the technique of MEG as well) might be effective in capturing the visual processing in the lower-tier, but not the higher-tier, areas. It is expected that the use of other stimulus configurations together with the combined use of MEG and fMRI (such as fMRI-constrained multiple-ECD analyses) may further elucidate the hierarchical processing stages of illusory-contour perception in the human visual cortex. Finally, the present results are also consistent with the psychophysical studies which have suggested that formation of illusory contours originates in the early and preattentive processes in the human visual system [1,5].

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