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Neural substrates for depth perception of the Necker cube; a functional magnetic resonance imaging study in human subjects

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Abstract

We have studied the cerebral activity for the depth perception of the Necker cube by functional magnetic resonance imaging. Three types of line drawing figures were used as stimuli, the Necker cube, hidden line elimination cube and overlapping squares. Subjects were instructed to perceive both orientations of the depth of the Necker cube. They were instructed to shift their attention voluntarily during viewing overlapping squares to obtain a control for the attentional shift in perceiving the Necker cube. A hidden line elimination cube was used as a control for monocular stereopsis. The results showed a clear symmetrical activation in premotor and parietal areas during the Necker cube perception compared with other conditions. The present result suggests that a neural process similar to mental image manipulation occurs during depth perception of the Necker cube. © 2000 Published by Elsevier Science Ireland Ltd. All rights reserved.

Keywords: Monocular stereopsis; Perception of depth; Line drawing; Necker cube; Functional magnetic resonance imaging; Parietal cortex; Premotor cortex

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Binocular stereopsis has been studied by neuroimaging, in order to clarify the neural substrates of binocular depth [13,11]. The perception of monocular stereopsis is important in the human visual system as well as binocular stereopsis, but there have been few neuroimaging studies on this topic. In the present functional magnetic resonance imaging (fMRI) study, we used the Necker cube and other line drawings as stimuli for examining monocular depth perception, as well as the cognitive mechanism during the perception of the Necker cube. There is a tendency to perceive the face of the Necker cube that includes the vertex nearest the visual fixation point as the frontal face [6]. Kawabata et al. [6] reported that, if the gross structure of figure permits two kinds of interpretations, it seems that the perception of the figure is strongly influenced by the prevalent interpretation of the local structure in the neighborhood of the visual fixation point. An experiment using a stabilized retinal image indicated that ambiguous depth perception of the Necker cube was independent of the fluctuations of eye movement [12]. Necker cube is, thus, an interesting problem with regard to both visual attention and depth perception.

Bisiach et al. [2] examined the depth perception of the Necker cube by groups of patients with or without left hemispatial neglect. The results showed that the deficits in the dynamic attention system of the hemispatial neglect patients strongly influenced deeply the perception of the depth ambiguity of the Necker cube. They proposed that a process like navigation in real space might be necessary for the disambiguation of Necker cube depth perception.

We used the Necker cube, a hidden line eliminated cube and overlapping squares as visual stimuli. Subjects were instructed to perceive both directions of depth voluntarily at each presentation of the Necker cube. In light of the results of Kawabata's study [6], the attention of the subjects should shift between the front and rear faces of the cube, in perceiving the depth of two directions. During viewing overlapping squares, subjects were instructed to pay attention to each square one by one, so that this condition should serve as a control for attentional shift. Both squares in the overlapping squares were shown at the same position as

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those shown in Necker cube. We adopted a hidden line elimination cube as a control stimulus because it is recognized as an object with depth even by monocular perception just as is the Necker cube.

Twelve healthy right-handed university students served as subjects and gave written informed consent after being fully instructed on the nature of the study. All subjects had normal vision. The stimuli shown in Fig. 1A–C were shown to the subjects (A; Necker cube, B; a cube with hidden line elimination, and C; overlapping squares). The objects were drawn in black and white and presented 3.6° of visual angle onto a screen set inside the MRI apparatus through a liquid crystal display projector controlled by a Macintosh computer.

Stimuli were presented in 16 blocks; the duration of each block was 24 s. There were four conditions, a Necker cube (condition N), a hidden line elimination cube (condition H), an overlapping squares (condition S) and fixation (condition F). The duration of each presentation was 2.0 s, separated by 1.0 s interval. Eight stimuli were presented successively in one block in the center of the screen. All the stimuli in the three conditions, N, H and S, were presented by rotating 0, 90, 180 or 270° in random order. In this experiment, the sequence of the blocks was counter balanced as F N S H F H S N F N S H F H S N. In the condition N, they were instructed to change voluntarily their perception of the orientation of the cube once during each presentation; in the condition S, they were instructed to shift voluntarily their attention from one square to the other during each presentation. The squares provided most of the information found in the Necker cube, but without necessarily a three-dimensional interpretation. The subjects were also instructed to fixate the center of the stimulus throughout the duration of the experiment.

Brain activity was measured during this time using a 1.5 T MRI scanner (GE, Horizon). Time-point of 128 single shot gradient echo echo-planer imaging images were obtained with TR = 3 s, TE = 40 ms, FOV 24 cm, matrix size 64 × 64 in 13 axial planes of 7-mm thickness and 1-mm gap. The functional image analysis was performed on a workstation using Statistical Parametric Mapping (SPM96, Wellcome Department of Cognitive Neurology, London, U.K.) implemented in MATLAB (Mathworks Inc., Natick, MA, USA). Scans were realigned using the first as a reference and were subsequently transformed into a standard space corresponding to the stereotactic atlas of Talairach and Tournoux using MNI templates (Montreal Neurological Institute). These normalized images were smoothed with an 8 mm full width at half maximum isotropic Gaussian kernel. Analysis was carried out using the general linear model with a delayed boxcar waveform. Any subject-specific low frequency drift in signal was removed by modeling with low frequency sine and cosine waves and global changes were removed by proportional scaling. Effects at each and every voxel were estimated and regionally specific effects were compared using linear contrasts. The resulting set of voxel values for each contrast constituted statistical parametric map of the t statistic SPM$\{t\}$ which was then transformed to the unit normal distribution, SPM$\{Z\}$ [5]. Statistical inferences were based on the theory of random Gaussian fields. Activations that were significant at $P <$ 0.05 corrected for multiple comparisons were reported. The stereotactic coordinates of Talairach and Tournoux [17] are used to report the observed activation foci.

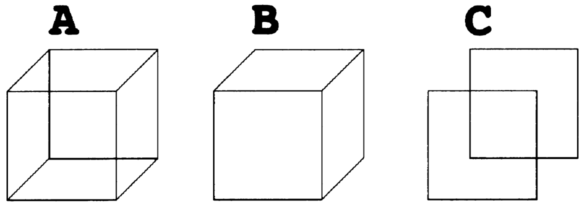

Fig. 1. Stimulus patterns used in the experiments: Necker cube (A), hidden line eliminated cube (B) and overlapping squares (C).

Comparison of the condition N with the other conditions, H, S and F, showed activation of bilateral parietal lobe, bilateral premotor area, bilateral occipitotemporal area, the left supplementary motor area (SMA) and posterior part of the left inferior frontal gyrus (Fig. 2).

The conditions N and S required shifts of attention in common, while the conditions N and H contained monocular stereopsis in common. Therefore, the comparison between condition N and H (the NH comparison) is thought to reflect the differences derived from the attentional shift, and the comparison between the conditions N and S (the NS comparison) is thought to reflect whether monocular stereoptic information processing occurred.

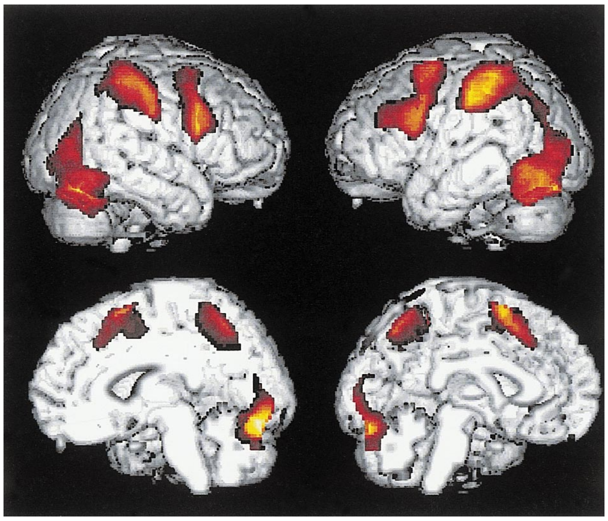

Fig. 2. Thresholded fMRI surface rendered activation images superimposed on standard structural images for twelve subjects in the comparison between the Necker cube condition and the fixation condition (voxel level $P < 0.001$, extent threshold $P < 0.05$). The four figures are, the right lateral view (top, left), the left lateral view (top, right), the medial view of the right hemisphere (bottom, left) and the medial view of the left hemisphere (bottom right).

The activation pattern was largely similar in both the NH and NS comparisons (Table 1). However, the SMA activation clearly seen in the NH comparison (Fig. 3, arrow 1, the Talairach coordinates of the peak activation; −6, 16, 50) is very weak in the NS comparison. Moreover, there is an activated area located in bilateral occipitotemporal gyrus in the NS comparison (Fig. 3, arrow 2, activation peaks; −42, −64, −8 (left), 42 −66, −20 (right)), which is not observed in the NH comparison. These differences might reflect a cognitive difference between the two comparisons. In the NS comparison there was activation in the right prefrontal lobe, which was not detected in the comparison between the Necker condition and the fixation condition. We, therefore, doubt that the activation is related to any phenomena of cognitive significance.

Previously, it has been known from neuropsychological studies that damage to the intraparietal sulcus and its neighboring regions in the superior parietal cortex can lead to optic ataxia. It is also known that damage to the right inferior parietal cortex can lead to deficits in the copying of solid objects [7].

The activation of bilateral premotor and parietal area was characteristic in our present results in the Necker cube perception compared with other conditions. These activated areas were very similar to those which were reported by Mellet et al. [10] in their positron emission tomography (PET) experiment for mental image manipulation task. They reported that bilateral parietal and bilateral premotor activation was detected during the task of mental image construction compared to the word listening condition. Moreover, it has been suggested that the left inferior parietal cortex may be involved in the motor image of hand movement and mental rotation [16,1]. Rosen et al. [15] reported a bilateral premotor and parietal activation in a task including both endogenous and exogenous attentional shifts in their fMRI study. They argued the activation of the premotor area might be involved in both voluntary and reflexive attentional shift to the periphery, since the activation was considered to have no relation to motor execution or preparation. Rizzolatti et al. [14] asserted that spatial attention is inextricably linked to the motor execution system. Recently, it was found that one of the important functions of the posterior parietal lobe in the monkey is the extraction of a variety of motor behavior, which means that visual cues are mapped directly to parameters that are relevant for motor function [4]. Consequently, mental imagery, such as reaching and/or grasping an object, and the possible somatosensory feedback from the imagery action might be important elements for the perception of visually presented objects. In addition, we

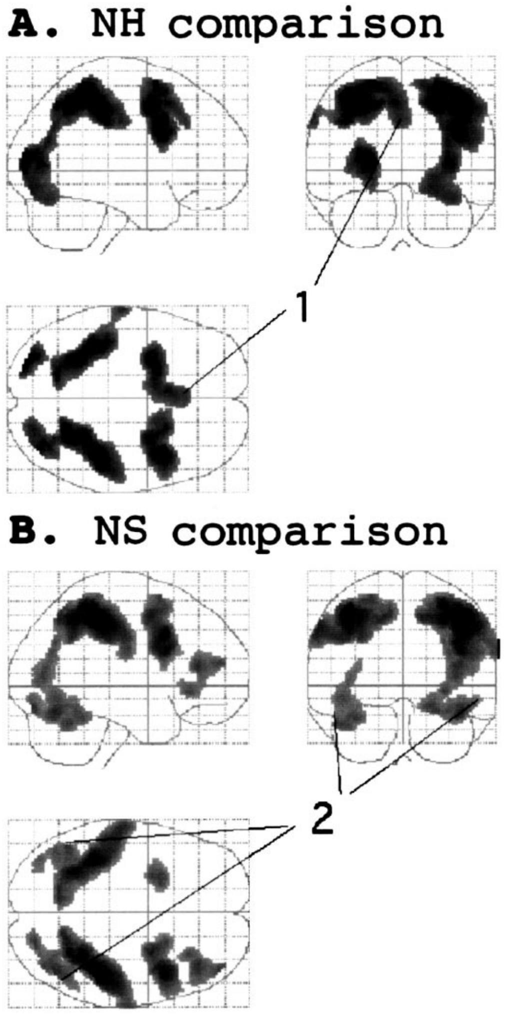

Fig. 3. Brain activation in the NH and NS comparisons shown in a translucent brain system. (A) NH comparison, (B) NS comparison (voxel level $P < 0.001$, extent threshold $P < 0.05$).

Table 1
Anatomical regions, peak voxel coordinates and *Z* scores of detected activation in NH and NS comparisons[a]

Anatomical region	Coordinates			*Z*
	x	*y*	*z*	
NH comparison				
R superior parietal lobule	28	−46	60	4.96
R inferior parietal lobule	44	−36	48	4.90
L inferior parietal lobule	−38	−40	54	4.88
L superior parietal lobule	−28	−50	52	4.78
L premotor area	−28	2	46	4.72
R premotor area	38	8	30	4.62
M frontal gyrus	−6	16	50	4.17
NS comparison				
R inferior parietal lobule	44	−36	46	5.76
R superior parietal lobule	28	−46	60	4.99
L inferior parietal lobule	−38	−40	54	5.29
L superior parietal lobule	−30	−52	50	4.87
R premotor area	40	8	32	4.85
L premotor area	−26	4	46	4.04
R middle frontal gyrus	42	50	16	4.09
R occipitotemporal lobe	42	−66	−20	4.26
L occipitotemporal lobe	−42	−64	−8	3.71

[a] Significance level was set at $P < 0.001$ ($Z > 3.09$) for voxel level and at $P < 0.05$ for cluster level. R, right; L, left; M, medial.

should mention the interpretation of the SMA activation seen in the result of the NH comparison (Fig. 3A1) and the bilateral occipitotemporal activation in the result of the NS comparison (Fig. 3B2). SMA activation has been reported in neuroimaging tasks which require subjects to make motor executions, especially voluntarily [8,3]. In our study, subjects were required to shift their attention in both of conditions N and S, but not in H. We consider the SMA activation seen in the NH comparison might be related to this difference, with or without the requirement of a voluntary attentional shift. On the other hand, there occurred bilateral occipitotemporal activation in the NS comparison but not in the NH comparison. The N and H conditions involve monocular stereoptic processing: both the Necker cube and the hidden line elimination cube were to be seen as an object with depth, while the overlapping squares were not. Therefore, the activation in the bilateral occipitotemporal gyrus might be related to the process of monocular stereopsis. Martin et al. [9] reported a similar activation pattern in this area in the comparison of two conditions, viewing non-sense objects (line drawings with stereoptic information) vs. viewing random dot patterns in their PET study.

In conclusion, bilateral premotor area and bilateral parietal cortex symmetrical activation might be involved in depth processing and attentional shift during viewing the Necker cube. These results suggest that the neural system formerly reported to be involved in motor imagery and the manipulation of mental imagery also plays an important role in the perception of visually presented objects. Moreover, by comparison among the three conditions, it was also demonstrated that an area involved in monocular stereopsis might exist in the bilateral occipitotemporal region.

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