An MEG study into the visual perception of apparent motion in depth

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Abstract

This study investigated (1) the responses associated with the perception of motion in depth induced by a series of scale-changing paradigms, and (2) the locations of the dipoles in the brain elicited by stimuli of motion in depth and in-plane motion. The former was determined using two types of stimulation: real motion and apparent motion in scale (AMS; where two frames with size-changed patterns were presented alternately); and the latter was determined by moving a full-field checkerboard pattern forward or rightward smoothly with the same time course. The results from analyzing magnetoencephalography (MEG) component M160 to differentiate the signals of perception can be summarized as follows: (1) the neurons stimulated by apparent motion (AM) might be similar to those stimulated by a real motion, since there was no statistical difference associated with the signals at M160 and the dipole locations; (2) the perceptional signal of motion in depth seems to be more sensitive when scale-changing information is present; and (3) asymmetrical responses are present in the visual system, with responses being more sensitive to expanding stimuli than to contracting ones, and with the activity being more prominent in the right occipitotemporal area. Overall, this study indicates that the responses evoked by the stimuli causing motion in depth are allocated more to area V3a rather to area V5.
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When an object moves through the visual field, its image slides across the retina and provokes the perception of motion. However, two discrete objects delivered sequentially with an appropriate displacement and timing can also cause the perception of smooth motion. This continuous motion sensation is called apparent motion (AM).

The human visual system is sensitive to the approaching objects in the lower visual field in order to detect threats from other animals at ground level [9,17]. Shirai and Yamaguchi [26] suggested that the visual system is more sensitive to motion which is toward the eye than away from it. This expansion of retinal images that supplied with motion-in-depth cues is very important in our daily life. Psychophysical and physiological studies have suggested that the visual system contains mechanisms for estimating motion in depth using different types of information, such as disparity, optic flow, and size changes [22,25]. Some researchers have assumed that optic-flow infor-mation is sufficient for computing motion (e.g., [3]), whereas others have suggested that scale-change information is used to estimate the expansion rate of the human visual system, with the optic-flow information used to improve the reliability (e.g., [25]). Therefore, the influence of scale-change information in the perception of motion in depth becomes an attractive issue.

It is commonly acknowledged that the human cortical area V5 is especially sensitive to motion stimuli [2,4,16,18,32]. Several studies have evidenced that neurons in this area have large receptive fields that can respond to the visual motion in a narrow range of directions and speeds [23,24]. Many studies have also suggested that AM is perceived – similar to real motion – in the same area [10–13,30]. In contrast, some other reports have indicated that area V3 shows a greater selectivity than area V5 to optic-flow stimuli [5–7,15,21,27]. Thus, it is still unclear whether the V5 area is the major stage to interpret the information of expansion or merely a relay station to integrate all motion information.

The technique of magnetoencephalography (MEG) records the magnetic fields due to neuronal activity in the living human brain [8]. The temporal resolution of this noninvasive method

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in recording neural activity is much higher than that for functional magnetic resonance imaging (fMRI) or positron emission tomography, and additionally the recorded signals pass through the skull and scalp without resistance so that it can provide better spatial resolution than electroencephalography (EEG). Therefore, it seems to be a more efficient tool to answer the above-mentioned question.

Seven healthy right-handed subjects (five males and two females) without ophthalmic and neurological abnormalities participated in this study. Their ages ranged from 23 to 27 years (24.6 ± 1.5 years, mean $\pm$ S.D.). All their visual acuities were corrected to the normal range (better than 20/25). Informed consents were obtained from all the participants.

In this study, we designed two experiments: (1) to examine the effect of scale changes for AM in depth in terms of the brain activities (amplitude and latency) around the M160 component [10,12,30], and (2) to identify the locations of dipoles elicited by different stimuli that form the perception of motion in depth or in-plane motion. In experiment 1, two types of stimulations were presented to the subjects: (1) for motion stimulation, a checkerboard pattern showed up for 400–500 ms and then moved forward (expanded from the smallest size of $1.6° \times 1.2°$ to the largest size of $25.6° \times 19.2°$) or backward (contracted from $25.6° \times 19.2°$ to $1.6° \times 1.2°$) at a constant speed for 100 ms followed by the end one for another 500 ms (Fig. 1(a)); and (2) for AM in scale (AMS), the first checkerboard pattern (window size: $6.4° \times 4.8°$; checker size: 1.25 cycles per degree) was displayed for 400–500 ms, which was followed by another frame that was displayed for 500 ms. This second frame had three types of modification (Fig. 1(b)): (i) AMS(a), in which the window size was changed to $25.6° \times 19.2°$ or $1.6° \times 1.2°$ and the checkers were rotated 45° with a size of 5 or 0.3 cycles per degree, respectively; this design was meant to disrupt the perception of approached motion by optic flow related to the original pattern; (ii) AMS(b), in which both the window and checker sizes were changed as given in (i) but without rotating checkers; and (iii) AMS(c), in which the window size was also changed as in (i) but the checker size was identical. In experiment 2, the motion stimuli were similar to those in Fig. 1(a) but with a full-screen checkerboard pattern (i.e., no surrounding background) displayed as moving forward (motion in depth) or rightward (in-plane motion) with the same time course.

The mean luminance of all the patterns was $6 \, cd/m^2$, which was the same as that of the gray background. Stimuli were generated by Presentation 0.55 NBS (Neurobehavioral Systems, Inc., CA, USA) with a personal computer and projected onto a transparent screen by a projector (Vista Pro, Electrohome Electronics). The pattern was viewed binocularly at a distance of 120 cm. Subjects were instructed to fixate on a small red cross present in the central field so as to minimize eye movement during the test without giving other tasks.

Visual evoked fields were recorded with a whole-head 306-channel neuromagnetometer (Vectorview, 4-D Neuroimaging, San Diego, CA). Vertically and horizontally bipolar electrooculograms (EOGs) were recorded at the same time as the magnetic-field data. Artifact rejection was performed by removing epochs with amplitudes exceeding 6000 fT/cm in the MEG or 300 uV in the EOG signals. The magnetic responses were digitized at a sampling rate of 512 Hz and filtered by a 1–40 Hz bandpass filter before further analysis. The mean signal level in the prestimulus period (100 ms) was defined as the baseline and treated as a dc offset. One hundred epochs were averaged for each test session.

The subject's head shape and position with respect to the MEG sensor were measured from four head-position indicator coils and a three-dimensional digitizer. Three predetermined landmarks on the scalp were also used to match and coregister MEG source signals on the anatomical magnetic resonance imaging (MRI) scans to constrain realistic source reconstruction according to the coordinate systems. The MRI images were acquired by a 1.5-T scanner system (Sonata, Siemens, Germany).

The equivalent current dipole (ECD) model in a spherical volume was applied to estimate the cortical sources of the measured magnetic fields. If the goodness-of-fit (GOF) was not more than 80% for the dipole fitting of the whole head, the boundary of the estimation (or the region of interest) was readjusted so as to reduce the noise from other regions of the cortex. We used three dipoles to model the whole field (around the occipital area, right temporal area, and left temporal area). The criteria used in this study to ensure good dipole fitting was the ECDs accounting for more than 85% of the GOF.
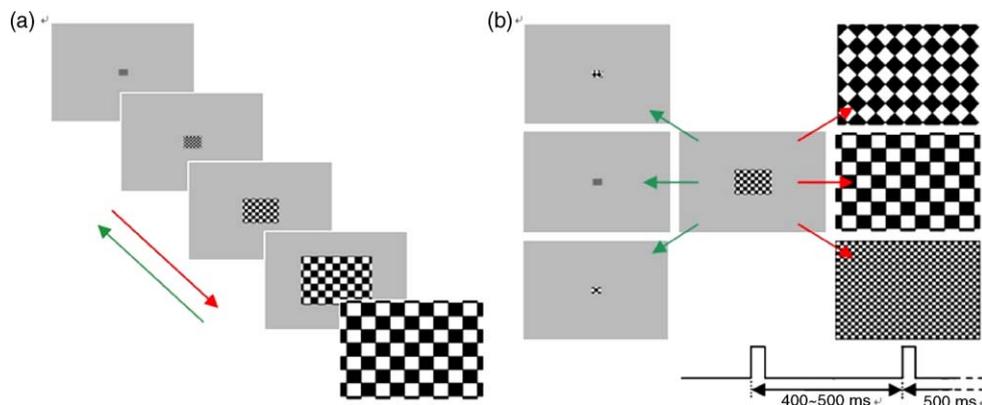

Fig. 1. The two types of stimuli used in this study: (a) motion and (b) apparent motion in scale. The time course of presentation is also shown.
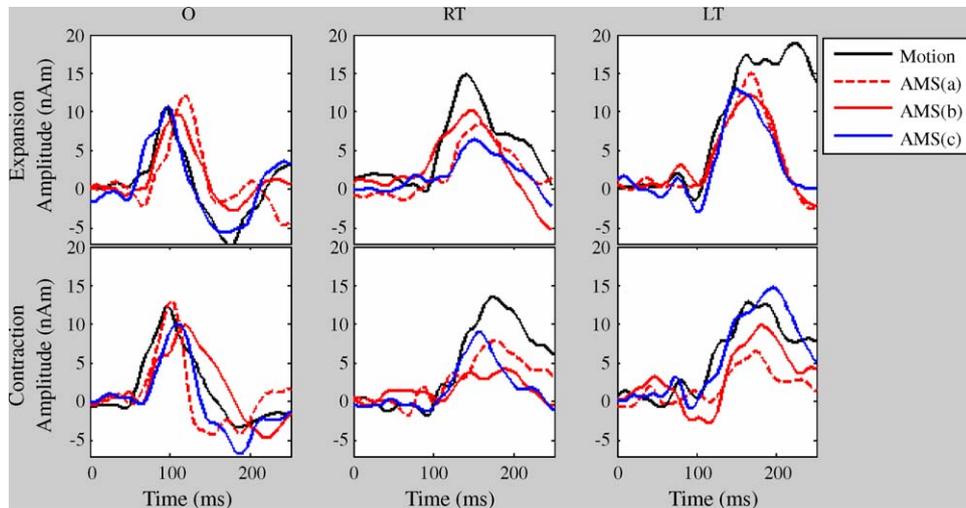
Fig. 2. The grand-average waveforms of all the subjects. The left, middle, and right plots correspond to fitting dipoles in the occipital, right temporal, and left temporal areas, respectively. The upper and lower plots represent expansions and contractions, respectively.

The nonparametric Wilcoxon signed-rank test was applied to analyze the responses of the stimuli to motion and AMS. The difference was taken as significant when the probability value (p) was <0.05.

The averaged source waveforms of all subjects in accordance with the spherical model and multiple-dipole ECDs around the occipital, right temporal and left temporal areas under different stimuli are shown in Fig. 2. The major components (M100) in the posterior occipital area to all stimulations were nearly identical in location, latency, and amplitude.

In the right temporal area, although the peak latencies of the M160 components were longer for the stimulation of contraction than that of expansion, the difference was not significant ($p > 0.05$). The peak amplitudes for expansions decreased in the following order: motion > AMS(b) > AMS(a) > AMS(c); with statistically significant differences between motion and AMS(c), and between AMS(b) and AMS(c). The peak amplitudes for contractions were relatively different in the order but still revealed significant differences between motion and AMS(c) (Table 1). In the left temporal area, the peak latencies of the M160 compo-

nents to all stimulations were approximately identical. However, the peak amplitudes only differed significantly between motion and AMS(c) for expansions, and between motion and AMS(a) for contractions.

In order to compare the responses induced by the above-mentioned stimulations, each dipole in the head coordinates of subjects was converted to the Talairach coordinates. The locations of ECDs were superposed on the MRI images. In the posterior occipital area, the dipoles were located around the calcarine fissure for all stimulations. In the right temporal area, the dipoles located on the x-axis were closer to the medial point in response to motion and AMS(b) than for the other expansions, whereas no significant difference was found for contractions. Meanwhile, the locations of the dipoles on the y- and z-axes did not differ between any of the stimulation types (Table 1). However, the interindividual variations in the locations of the dipoles were greater in the left temporal area than in the right temporal area.

The criteria of three-dipole fitting were applied to the magnetic-field distributions, but only focusing on the right

Table 1
Features of the fitted dipole around the right temporal area to different stimuli

	Mode	Motion	AMS(a)	AMS(b)	AMS(c)
Latency (ms)	Expansion	160.6 ± 27.2	158.6 ± 29.2	154.6 ± 21.0	165.0 ± 21.3
	Contraction	176.8 ± 22.6	185.3 ± 25.9	173.6 ± 36.7	155.3 ± 9.6
Amplitude (nA)	Expansion	20.3 ± 15.6	10.7 ± 6.9	14.4 ± 6.8	8.8 ± 4.6[#]
	Contraction	17.9 ± 12.0	11.1 ± 6.0	9.4 ± 1.8	10.3 ± 5.3[*]
x-axis (mm)	Expansion	19.8 ± 6.2	33.2 ± 5.8[*,#]	25.1 ± 10.4	34.5 ± 5.6[*,#]
	Contraction	25.4 ± 10.9	24.3 ± 6.0	24.4 ± 5.3	28.0 ± 5.0
y-axis (mm)	Expansion	−79.7 ± 11.4	−55.4 ± 24.2	−64.7 ± 14.5	−69.0 ± 17.6
	Contraction	−73.8 ± 11.3	−79.3 ± 3.9	−73.3 ± 4.0	−72.4 ± 10.3
z-axis (mm)	Expansion	11.7 ± 7.0	7.7 ± 12.9	15.43 ± 8.2	15.8 ± 14.3
	Contraction	8.7 ± 10.6	12.2 ± 5.0	19.1 ± 5.4	20.2 ± 11.2

[*] Indicate a significant difference ($p < 0.05$; paired Wilcoxon signed-rank test) relative to motion.
[#] Indicate a significant difference ($p < 0.05$; paired Wilcoxon signed-rank test) relative to AMS(b).

temporal area. The peak latencies of the M160 components caused by the stimulus of in-plane motion (181 ± 29.8 ms) were relatively longer than those stimulated by motion in depth (165 ± 20.1 ms), but no significant difference was observed statistically. However, in the spatial domain, dipoles located on the x-axis were closer to the medial point for motion in depth (22.59 ± 7.58 mm) than for in-plane motion (43.02 ± 4.66 mm). Similarly, on the y-axis, the dipoles were more posterior for motion in depth (-80.74 ± 2.36 mm) than for in-plane motion (-61.86 ± 7.91 mm). The dipole location on the z-axis did not differ for all stimulation types.

In this study the peak amplitudes of the M160 component for expansions in the right temporal area decreased in the following order: motion > AMS(b) > AMS(a) > AMS(c). This suggests that, first the neural responses to the stimuli of AMS are smaller but similar to those of the motion stimulus. This relationship between AM and motion is similar to that reported by Kobayashi et al. [11]. Hence, according to the results described above, it is suggested that AM and motion stimulate similar neurons. Second, the perception of motion in depth seems to be more influenced by AMS(a) than by AMS(c). Similar experiments performed using limited-lifetime random-dot kinematograms produced similar results (data not shown). This implies that the expanded pattern could convey the information to generate the perception of motion in depth irrespective of whether the pattern is like the original. In general, it seems that changing the scale of objects is more effective than the other types of stimulations at inducing a motion-in-depth perception. This result is in agreement with a psychophysical study [25] involving the use of stochastic texture stimuli in a random optic-flow pattern. Third, the human visual system can respond asymmetrically to visual stimuli, as detected by comparing the responses to expan-

sions and contractions—the variation in amplitude is greater for the latter than for the former. This is consistent with results from other studies [17,26], and indicates that the requirement for the sensitive perception of approaching objects is a natural protection mechanism for human beings. Such approaching objects, especially in the lower visual field, might represent potential dangers or predators. The other asymmetry is that the response is dominated in the right occipitotemporal area. Some studies using different measurement techniques for various visual-motion stimuli have also found that bilateral activities predominate in the right hemisphere [11,18,29,31]. This asymmetry might be considered to be a fundamental difference between the two hemispheres, with the left hemisphere specialized in linguistic and logical processing and the right hemisphere generalized in spatial processing. Although this dichotomy is probably too simplistic since the brain exhibits plasticity, data from split-brain patients do explain some of those observations.

We found that dipoles located on the x-axis were significantly more medial in motion and AMS(b) than for the other types of expansions. Since the responding locations are quite different between AMS(b) and AMS(c), it is possible that the pattern for AMS(c) could not stimulate the perception of motion in depth. In addition to areas V1 and V2, most investigators now recognize that all primates have an MT (or V5) area. Diverse visual stimuli, such as motion translation, rotation, stereopsis, and illusion of motion, are known to activate this area [1,30]. Although area V5 is conventionally thought to be more related to motions, area V3 seems to be more sensitive to motion in depth [5–7,15,21]. In the hierarchical view of the dorsal stream, V3/V3a and V5 (middle-tier areas) make the connections between lower visual areas (V1 and V2) and higher visual areas (MST and V7). Since human responses to complex motions were largest for expan-
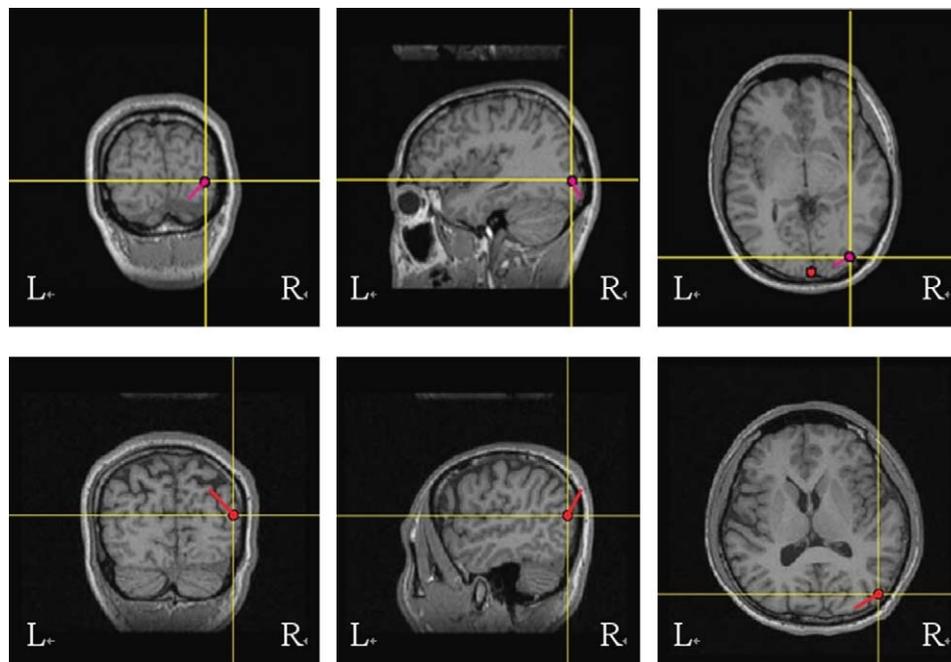

Fig. 3. Two-dimensional MRI images superposed with the estimated ECDs of the MEG responses with respect to different stimuli in one subject. The upper images correspond to forward motion ($x = 20$, $y = -80$, $z = 12$). The red point is the first dipole fitted around the calcarine fissure. The lower images correspond to rightward motion ($x = 41$, $y = -73$, $z = 19$).

sions [9], this type of information should be processed earlier than other motion conditions. Thus, the above-mentioned discrepancy might be due to a basic difference in the areas that responded to different types of motion stimuli. This explains why the dipoles induced by AMS(c), for which it was difficult to elicit a perception of motion in depth, are located much closer to area V5 than area V3. However, there are some differences between humans and monkeys in area V3 [19,20,28,33]: V3 is more motion selective than V3a in macaque, but vice versa in human; and this was verified in experiment 2 of the present study. According to the template (in Talairach coordinates) described in [5,14,15,21], the mean coordinates in the right hemisphere are (21, −92, 10) for area V3 (dorsal cuneus or BA 19), (22, −88, 13) for V3a, and (45, −70, 3) for V5 (medial temporal lobe or BA 37). Our results confirm that the responses elicited by stimuli aimed at perceiving motion in depth are located around area V3a, while the responses for in-plane motion are near area V5 (Fig. 3). This suggests that area V5 acts as a relay station that integrates all motion information rather than being the first stage to conduct information related to motion in depth.

In conclusion, the results from the present study suggest that similar cortical areas are stimulated by AM and real motion, and patterns with a changing size more readily induce the sensation of motion in depth. Two asymmetries of the visual responses were observed, one caused by different stimulated patterns of expansion and contraction, and the other is the perception of motion in depth due to a given stimuli being dominated by the right hemisphere. Finally, the present results also indicate that motion in depth evoked responses closer to area V3a than to area V5.

Acknowledgments

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