Physiological Evidence of Interaction of First- and Second-Order Motion Processes in the Human Visual System: A Magnetoencephalographic Study

Ayako Sofue,^{1,2} Yoshiki Kaneoke,^{1*} and Ryusuke Kakigi¹

¹Department of Integrative Physiology, National Institute for Physiological Sciences, Okazaki, Japan

²Department of Pediatrics, Nagoya University School of Medicine, Nagoya, Japan

Abstract: Humans have several mechanisms for the visual perception of motion, including one that is luminance-based (first-order) and another that is luminance-independent (second-order). Recent psychophysical studies have suggested that significant interaction occurs between these two neural processes. We investigated whether such interactions are represented as neural activity measured by magnetoencephalography (MEG). The second-order motion of a drifting sinusoidal grating, which is defined by the speed of the dot motion, did not generate a response. Apparent motion (AM) of the square area, defined by the speed of randomly moving dots, evoked a magnetic response whose latency and amplitude changed with the distance that the area moved (a second-order characteristic), though the response properties were significantly different from those for the first-order AM. AM, defined by both first- and second-order attributes, evoked an MEG response and the latencies and the amplitudes were distributed between those for the first- and second-order motions. The cortical source of the response was estimated to be around MT+. The results show a distinct difference in the neural processing of the second-order motion that cannot be explained by the difference in visibility, and they indicate that the interaction of the neural processes underlying first- and second-order motion detection occurs before the MEG response. Our study provides the first physiological evidence of a neural interaction between the two types of early motion detection. *Hum. Brain Mapp.* 20:158–167, 2003. © 2003 Wiley-Liss, Inc.

Key words: apparent motion; motion-defined motion; MT/V5; sinusoidal grating

INTRODUCTION

Our visual system usually detects moving objects because they are brighter or darker than the background. However, it is known that humans can perceive the motion of an object whose surface luminance is the same as that of the back-

ground. These facts have led to the idea that humans have several distinct motion detection mechanisms [Cavanagh and Mather, 1989; Chubb and Sperling, 1988; Lu and Sperling, 1995, 2001]. One type is luminance-based (first-order) and the other is a mechanism (second-order) that extracts motion from other attributes such as texture and contrast. A number of psychophysical studies [Ashida et al, 2001; Harris and Smith, 1992; Ledgeway and Smith, 1994; Nishida et al., 1997; Scott-Samuel and Georgeson, 1999; Scott-Samuel and Smith, 2000] and human case reports [Plant et al., 1993; Vaina et al., 1999] indicate that the neural processing underlying the second-order motion is functionally and anatomically segregated from that responsible for the first-order motion. Recent studies [Harris and Smith, 2000; Lindner and Ilg, 2000;

*Correspondence to: Dr. Yoshiki Kaneoke, Department of Integrative Physiology, National Institute for Physiological Sciences, Myodaiji-cho, Okazaki, 444-8585, Japan. E-mail: kaneyo@nips.ac.jp

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Smith and Scott-Samuel, 2001; Zanker and Burns, 2001], however, have elucidated non-trivial interactions between the two neural processes; such interactions are not entirely surprising because we rarely observe moving objects whose motion can be considered exclusively first- or second-order.

Several models [Lu and Sperling, 2001; Nishida and Sato, 1995; Schofield and Georgeson, 1999; Wilson et al., 1992; Zanker and Hupgens, 1994; Zhou and Baker, 1993] have been proposed to explain the various properties of second-order motion perception, though there is little physiological evidence to support these ideas. These models have two common features: one is preprocessing prior to the calculation of the second-order motion, and the other is integration of both first- and second-order information at a certain stage of the motion perception process. Because objects perceived by the second-order system are defined by the spatial and temporal variation of their luminance (or color), these objects must first be detected by some neural process, referred to here as “preprocessing,” before their motion can be perceived. This preprocessing must be independent from the detection of first-order motion. At later stages, these two motion detection systems seem to communicate with each other, because the existence of one type of motion affects the perception of the other.

In this study, we investigated whether integration of both first- and second-order motion information occurs and, if so, how and where in the human brain such a neural process is performed, using magnetoencephalography (MEG). In our previous studies, we found that various visual motion stimuli evoked MEG responses from the extrastriate cortex (probably including human MT/V5), and that the response latencies and amplitudes changed dynamically with stimulus conditions such as motion speed [Kaneoke et al., 1997; Kawakami et al., 2002; Maruyama et al., 2002]. If the human brain requires preprocessing for the detection of second-order motion, its response latency should be longer than that for first-order motion, and the time course of the response properties should differ from each other. Furthermore, we compared the response to motions that have attributes of both first- and second-order motion (mixed motion) with the response to pure first- and second-order motions alone. If the interaction of the neural processing underlying the first- and second-order motion detection systems occurs before the response from the human MT/V5, the response properties for the mixed motion should be different from those for the other two types of motions, which could not be explained by the linear summation of the responses to the first- and second-order motions.

Although there are many different ways to present second-order motion [Baker, 1999], we used the difference in the speed of randomly moving dots. The detection of this second-order motion requires explicit preprocessing, because the object is defined by a first-order motion [Zanker and Burns, 2001]. Theoretically, it is possible to consider a neural system that detects both first- and second-order motion when the second-order motion is defined by attributes other than local motions [Chubb and Sperling, 1988;

Johnston et al., 1992]. This implies that the difference in the neural processing between the two types of motion is too small to be detected by the available methodology. In contrast, second-order motion of an object defined by local motions requires explicit preprocessing. With this type of second-order motion, we may be able to measure the neural activity related to the preprocessing of this motion perception, because the preprocessing in this case would be enhanced more than that underlying other motions. Furthermore, the second-order motion in this study is theoretically immune to any first-order artifact, that is, the small local luminance change at the boundary of the objects defined by other second-order attributes such as texture [Chubb and Sperling, 1988; Smith et al., 1998].

MATERIALS AND METHODS

Subjects

We selected three subjects (one woman, two men; age 28–43 years) for the present study from 12 colleagues, based on their MEG response amplitudes for first- and second-order sinusoidal motion and second-order apparent motion with a spatial separation of 2 degrees. Informed consent was obtained prior to this study. All subjects had normal or corrected-to-normal visual acuity.

Visual Stimulation

We used a random dot kinematogram (RDK) to generate various first- and second-order visual motion stimuli. Because the main purpose of this study was to investigate in detail the human cortical response to second-order motion, the first-order motions were created by adding first-order artifacts (that is, differences in the luminance) to the second-order motions so that we could parse the responses into those with or without first-order artifacts. All stimuli were generated by an IBM compatible PC and were projected onto a screen using an LCD projector (LP-9200; Sanyo, Japan). The resolution was 640×480 pixels at 60 Hz and all the pixels were refreshed with each frame irrespective of the next frame image.

Two types of motion were used to measure the temporal structure of the cortical responses to the onset of motion using MEG. One was the smooth motion of a drifting sinusoidal grating and the other was the apparent motion of a square area (Table I and Fig. 1). Initially, the study was done with a sinusoidal grating alone, but the second-order motion of the sinusoidal grating did not evoke an MEG response, leading us to add the apparent-motion stimulus.

For both motion types, first-order motion was presented as luminance changes and second-order motion was accomplished by modulating the speed of the dots' motion. The dot density of the stimulus was always 10% and a dot corresponded to a single pixel brighter than the background. The stimuli were presented on a screen in a magnetically shielded room through a small window. The stimulus subtended a visual angle of 7.7×7.7 degrees and employed a

TABLE I. Stimulus conditions used in this study

Stimulus	Attributes of the object
SMx	Dot speed and luminance are sinusoidally modulated
SM2	Dot speed is sinusoidally modulated
AM1	Dots in the square area are brighter than those in the background ^a
AMx	Dots in the square area are brighter and faster than those in the background ^a
AM2	Dots in the square area are faster than those in the background ^a

Offset responses to the square areas defined by the three apparent motion attributes were also measured.

^a All dots are moving randomly with a constant speed.

180 × 180-pixel array on the projector screen at a viewing distance of 200 cm. The fixation point, a 1 × 1-pixel red spot, was always shown so that all the stimuli were presented in the left visual field of the subject. This setup was based on our experience that the response waveforms are unnecessarily complex when stimuli are presented at the center of the visual field, and that the response amplitude is larger when the stimulus is presented on the left rather than the right. Furthermore, it is known that apparent motion is difficult to detect when the fixation point is between the two object squares [Kolers and von Grunau, 1977].

Smooth Motion (SM)

A drifting sinusoidal grating defined by the dots' speeds was used to present the second-order motion (SM2) (Fig.

Figure 1.

Schematic illustrations of the visual motion stimuli used in this study. **A:** Smooth motion of the second-order sinusoidal gratings (SM2) was defined by the sinusoidally modulated speed of the dots' motion, whereas the first-order motion (SMx) was defined by both sinusoidally modulated luminance and dot speed, as indicated by the sine wave shown under the stimulus. **B:** Apparent motion of the square area was defined by one of three attributes relative to the background. The background dots moved randomly at a speed of 2.6 deg/sec. Frame 1 was presented first for 2 sec and suddenly disappeared when Frame 2 appeared, which was presented for 1 sec and was followed by Frame 3. The square area in

Frame 2 was presented with a leftward shift of 0.5, 1, 2, and 4 degrees from the square area in Frame 1. For the first-order motion stimulus (AM1), the area was defined by a greater luminance of the dots in the stimulus area relative to the background. For the second-order motion stimulus (AM2), the area was defined by a threefold increase in the speed of the randomly moving dots relative to the background. For the mixed apparent motion stimulus (AMx), the area showed both properties. For the measurement of offset responses of the square area under the three stimulus conditions, Frame 2 was replaced by Frame 3, which had no defined square area.

1A). Each dot jumped either up or down a certain distance ranging from one to three pixels in each frame, which corresponded to a dot speed of 2.6 to 7.7 deg/sec. The dot's speed of motion was modulated sinusoidally at a spatial frequency of 0.4 cycles/deg. This sinusoidal grating drifted leftward at a speed of 2.6 deg/sec. The subject looked at the non-drifting sinusoidal grating for 2 to 3 sec before the onset of the drifting, which lasted for 0.5 sec. In each experimental session, this stimulation sequence was repeated 120 times to acquire more than 100 MEG responses for each subject and session.

The other smooth motion used (SMx) was similar to SM2, except that luminance modulation was added to the dots so that a faster dot was also brighter. The maximum luminance of the dots was 2.6 cd/m² (same as the luminance of the dots used in SM2) and the minimum was 2.4 cd/m². Thus, the global luminance of SMx was lower than that of SM2.

Apparent Motion (AM)

We used three types of apparent motion (AM1, AM2, and AMx) of a square area defined by three sets of attributes upon a background of dots randomly moving at a speed of 2.6 deg/sec: (1) the speed of the dots (AM2), (2) their luminance (AM1), and (3) both speed and luminance (AMx) (Fig. 1B). For second-order apparent motion (AM2), the square area was defined by a higher dot speed (7.7 deg/s), with the luminance kept at 2.6 cd/m², the same as the background. For first-order AM (AM1), the square area was defined by an increase in the brightness of the dots (2.6 cd/m² compared to 2.4 cd/m² for the background dots), but all the dots moved at the same speed (2.6 deg/sec). Apparent motion of the area defined by both attributes together was also used and is referred to as mixed AM (AMx). The size of the square was always 1×3.4 degrees and was located 1 degree from the fixation point. This square area (Fig. 1B, frame 1) was presented for 2 sec before it disappeared and the other square area (Fig. 1B, frame 2) was presented with a leftward shift of 0.5, 1, 2, or 4 degrees from the location of the first square. There was no interstimulus interval (ISI). The second area was presented for 1 sec and no area was presented (Fig. 1B, frame 3) for 1 sec before the next presentation of Frame 1. In each MEG data acquisition session, this stimulus sequence (Fig. 1B, frame 1, frame 2, and frame 3) was presented 120 times using one of four shifts of the area to record the response to the motion of the area from the first to the second location (i.e., in the direction away from the fixation point). For comparison with the response to apparent motion, simple offset responses to the square area in Frame 1, modulated in the three manners used in AM1, AM2, and AMx, were also measured. The stimulus sequence of this session was the same as that for AM except that Frame 2 (Fig. 1B) was omitted (i.e., Frame 1 was followed directly by Frame 3).

MEG Data Acquisition and Analysis

We used a 37-channel neuromagnetometer (Magnes, BTi) to record the magnetic fields from the right occipitoparieto-

temporal region of each subject's brain. Each subject lay on his or her right side on a bed in the dimly lit magnetically shielded room and was instructed to gaze at the fixation point located on the right side of the visual stimulus at a viewing distance of 200 cm. The subjects practiced the timing of blinking beforehand. Although we monitored the eye movements using an electrooculogram, it did not reliably measure small eye movements of less than 0.2 degrees. Rather, we could evaluate the subjects' eye fixation by the high S/N ratio of the averaged responses. Blink artifacts were discarded in the off-line analysis.

The magnetic field response data of 50 msec before and 700 msec after the onset of motion were amplified, filtered (0.1–800 Hz) and digitized at a sampling rate of 2,083.3 Hz until 120 and 240 epochs of data for AM and SM, respectively, were collected. The data for each epoch were averaged and the baseline for each channel was corrected for the mean level at 50 msec before the onset of motion. The data were then filtered in the range of 1–50 Hz for further analysis. In the off-line averaging, MEG responses with a drift of more than $\pm 1,500$ fT were discarded. The peak latency and amplitude of the first component of the magnetic response were measured as root mean square (RMS) values across the averaged response data of the 37 channels [Kawakami et al., 2002]. The single equivalent current dipole (ECD) model was used to estimate the location of the cortical activities that produced the magnetic fields [Sarvas, 1987]. We had two criteria for the application of the ECD model [Kaneoke et al., 1997]. First, the estimated ECD must be stable (within 5 mm of each coordinate) for at least 10 msec within 20 msec around the peak. Second, the correlation coefficient between the recorded magnetic field and values expected from the ECD model must be more than 0.95. The mean location of the estimated dipole during that period was calculated for each magnetic response. The 95% confidence distance of the dipole location for each subject was calculated as the mean distance + 1.96 SD between the mean and the estimated dipole location for each response. For the anatomical investigation of the estimated dipole location, 1.5-mm-thick, T1-weighted sagittal magnetic resonance images (MRI) were obtained with a 1.5-T MR imager (Shimadzu Medical Systems) as in our previous study [Bundo et al., 2000; Kawakami et al., 2002].

Because the 37-channel MEG system does not cover the whole brain, the first response may occur outside the measurement areas. The cortical source estimation for the response may also be affected by the coverage of the measurement areas. Thus, we performed an additional MEG experiment with the 306-channel whole-head MEG system (Vectroview; Neuromag Ltd., Helsinki). The stimulus conditions were the same as those for the 37-channel MEG, except that the subjects were sitting. Three subjects participated in this study, and S1 had measurements with both MEG systems for comparison. The cortical source of the response was estimated using the multiple-current dipoles model and the minimum current estimate [Uutela et al., 1999].

RESULTS

All the subjects perceived vivid motions effortlessly with all the stimuli used in this study. However, the response to the sinusoidal gratings was poor. Two subjects (S1 and S3) had measurable responses to SM1, but SM2 did not elicit a detectable response in any of the three subjects (Fig. 2). We measured the response to this stimulus in 12 other colleagues, but no one displayed a detectable MEG response. The peak latencies and amplitudes of the responses to SM1 were 309–329 msec and 28–47 fT, respectively.

In contrast, all apparent-motion stimuli, except for AM2 at a spatial separation of 0.5 degrees, evoked clear MEG responses from all the subjects. Figure 2 shows the waveforms of the responses to the various apparent-motion stimuli at 2 degrees from one subject. The peak latency of the first component of the response to AM2 (~290 msec) was markedly longer than that for other stimuli (~200 msec), and its associated peak amplitude was the smallest. The peak latency and the amplitude change with the spatial separation for each subject are shown in Figure 3. The peak latency tended to decrease as the spatial separation increased (F-ratio = 4.1, $df = 2$, $P < 0.05$ by three-way ANOVA, general linear model in SYSTAT). We also noticed some stimulus type-specific effects: the peak latency for AM2 tended to be approximately 100 msec longer than that of the other stimuli, and AM1 elicited the shortest latency (F-ratio = 85.2, $df = 2$, $P < 0.001$). The peak amplitude was also related to the spatial separation (F-ratio = 6.5, $df = 2$, $P < 0.01$); AM1 exhibited the largest amplitude, and AM2 the smallest (F-ratio = 29.9, $df = 2$, $P < 0.001$). All of the above statistical examinations were conducted excluding the data obtained using stimuli with a spatial separation of 0.5 degrees, because the data for AM2 are missing for this condition.

The difference in response properties between first- and second-order motions is clear when the relationship of the latency and the amplitude is examined. Figure 4 shows the correlation between the mean response rate (reciprocal of the latency), as done in our previous study [Kawakami et al., 2002], and the mean amplitude across the three subjects for the three different apparent motions. The numbers next to the plots represent the spatial separations. The amplitude correlated with the response rate for all the motions and was generally dependent upon the spatial separation. As can be seen, the distribution of the data for the second-order motion (AM2) is markedly different from that for the first-order motion (AM1), whereas the mixed motion (AMx) lies intermediate between the two. Note that the response properties of the offset responses are quite different from those of the other data. That is, the data for the offset responses could not be predicted by simple extrapolation of the spatial separations. Rather, these data were distributed within a small area on this coordinate system irrespective of the motion type. Discriminant analysis revealed significant differences in the distributions of the data for AM1, AMx, AM2, and the offset responses ($P < 0.001$).

The MEG responses from two subjects (S1 and S3) were used to estimate the cortical source localization using the

Figure 2.

Time courses of waveforms (starting at time 0) of MEG responses to the drifting sinusoidal grating (**left**) and apparent motion stimuli (**right**), with a distance of 2 degrees for a single subject, S1. Although the first-order smooth motion stimulus (SMx) evoked a response peaking at about 310 msec, there was no response to the second-order smooth motion stimulus (SM2). The first-order apparent motion stimulus evoked the response with the highest peak amplitude and the shortest latency. The peak latency of the response to the second-order apparent motion stimulus was approximately 100 msec longer than that of the others. The arrowhead indicates the peak of the response.

single ECD model. All the locations lay within a small region around the upper limb of the inferior temporal sulcus. Figure 5 shows the estimated dipole locations for the three apparent motions on the two- and three-dimensional brain images created by the anatomical MRI for the subject S1. The results of the cortical source estimation using the minimum current estimate for the peak responses measured with the whole head MEG are shown in Figure 6. Although the peak latencies were very different from each other (70 msec), both the responses were estimated to originate from the same occipitotemporal area.

DISCUSSION

Our present MEG study revealed marked differences between the response properties of first- and second-order motion. Although first-order motion of the sinusoidal grating (SMx) evoked responses, second-order motion (SM2) did not, probably because the response amplitude was below the noise level (about 20 fT for our MEG system). The low amplitude of the response to the second-order motion (SM2) was probably not simply due to low visibility, because the global luminance of SMx was lower than that of SM2. That visibility alone does not correlate with magnitude of MEG response to motion was shown clearly by the apparent motion study: the mixed apparent-motion stimulus (AMx), despite being more visible than either AM1 or AM2 alone, because it contains both sets of information together, exhibited latency and amplitude values that were distributed between the data for AM1 and AM2.

Figure 3.

Relationship between the peak latency (**A**) and the amplitude change (**B**), and the spatial separation of the apparent motion for the first component of the response to each stimulus (triangles, AM1; squares AMx; circles, AM2). For all the subjects (S1, S2, and S3), there was no response to AM2 with a separation of 0.5 deg. The peak latency was inversely related to the spatial separation (P

< 0.05) and differed significantly among the stimuli ($P < 0.001$). The peak amplitude was directly related to the spatial separation ($P < 0.01$) and differed significantly among the stimuli ($P < 0.001$), with the highest values achieved in response to first-order apparent motion. Note that the data for the offset responses were different from those for the largest spatial separation (4 degrees).

Our results show that the addition of a small luminance modulation to the second-order motion stimulus markedly changes its MEG response properties. The reason why a previous evoked-potential study [Victor and Conte, 1992] did not reveal any differences between the responses to first- and second-order motion is not known. This might be simply because the responses did not differ in their electrical field representations on the skull, but only in their evoked magnetic fields. The other possibility is that the second-order motion stimulus they used did not elicit as much of a differential response as the first-order motion, due to intrinsic second-order attributes, or because of unexpected first-order artifacts. Indeed, recent visual evoked potential study revealed the significant difference in the response latencies between the first- and second-order motions even though both motions had the same visibility [Ellemberg et al., 2003].

For all three apparent-motion stimuli, the response latencies and the amplitudes changed with the spatial separation. These results indicate that the responses were related to the motion and not merely due to the sequential presentation of the objects. Indeed, these response properties were different from the offset responses (see Fig. 4). It should be noted that the object (square area) in AM2 is defined by the local motion speed of the dots. Because the dots' motion directions were random as those in the background, the area was

Figure 4.

Relationship between the reciprocal of the response latency (response rate) and the peak amplitude of the response to all apparent motion stimuli. The data for the spatial separation of 0.5 degrees are not shown because no data were obtained for AM2. The number beside the plot shows the spatial separation. The amplitude is related to the response rate and the spatial separation. Note the difference in the distribution of the data with the motion types. In contrast, the offset responses are distributed in a small area.

Figure 5.

The estimated response source locations for the activity in response to the three types of apparent motion shown on two- and three-dimensional MRI images from subject S1. The nearest cortical surface is shown for each location on the 3-D MRI. Each colored dot indicates the cortical location corresponding to the response to a single motion stimulus. All colored dots were clustered around the ascending limb of the inferior temporal sulcus.

differentiated only by the speed difference. The fact that the area could be detected and evoked the apparent motion perception supports the view that the local speed information (as well as direction information) can be spatially integrated in the human visual system [Lam et al., 2003; Maruyama et al., 2002]. Interestingly, the offset response properties were similar irrespective of the stimulus type. This suggests that the representation of the cue-invariant form (the square area in this case) exists in a neural population and that the same neural activity can inactivate such a population even if the activation process of the neural group varies with the cue. That is, an offset response can be the same even though the onset response properties, the manner by which the area is defined, depend on the cue.

The dependency of latency on spatial separation seen in this study corresponds to the results of our previous studies [Kaneoke et al., 1998; Kawakami et al., 2000], where, in contrast to the current study, we used as a stimulus the apparent motion of a bar presented by an LCD projector and found a dramatic dependency of latency on spatial separation. In another experiment, we also observed this relationship with respect to the spatial separation of a light spot from a laser beam [Kawakami et al., 2000]; however, the latency changes were not as dramatic as those observed with the bar stimuli. Why we saw such a dramatic latency change only with the bar stimuli is not known, but the stimulus presentation system may have been somehow flawed, thus augmenting intrinsic latency changes.

The fact that the response latency to second-order AM is markedly longer than that to first-order AM may be related to preprocessing for the detection of second-order motion. Our present results correspond well to a recent psychophysical study indicating that the visual search rate for various

Figure 6.

The distribution of the cortical currents corresponding to the magnetic responses to both AM1 and AM2 for subject S1. The data are shown at the point of their peak latencies (195 and 265 ms) on meshed brain-surface models. The spatial separations were 2 deg for both stimuli. Although the peak latencies differed significantly

from each other, the estimated currents were distributed around the same occipitotemporal area. Dipole analysis indicated the same cortical area for the response sources (not shown). Current strength is indicated by color and varies from yellow (highest) to blue (lowest).

types of second-order motion is much slower than for first-order motion [Ashida et al., 2001]. The authors also showed that such low search rates were not due to lower visibility of the second-order motion stimuli. Although we did not investigate the visibility of the motion stimuli used in this study, lower visibility of second-order motion cannot underlie the longer response latency, as discussed above.

The response properties for the mixed motion (AMx) were distributed between those of the first- (AM1) and second-order (AM2) motion stimuli (Fig. 4). This indicates the existence of an interaction between the two neural processes underlying first- and second-order motion. A different response than what was observed would be expected in the absence of such an interaction. Since first-order motion processing occurs faster than second-order processing, if there were no interaction of the neural pathways before the response, the response evoked by AMx would be biphasic, with an early component identical to the response to AM1, followed by a slower component that would resemble the AM2 response.

Such interaction of the first- and second-order neural processing pathways underlying the response to AMx must occur before the response to AM1 is evoked. The cortical source of the response to first-order motion is thought to lie near the occipitotemporal area (including MT+), as seen in this study (see Figs. 5 and 6) and in previous studies [Kaneko et al., 1997; Kawakami et al., 2002]; therefore, the interaction probably occurs at an earlier stage of motion analysis, which is thought to take place in V1 and V2 [Smith and Snowden, 1994; Zhou and Baker, 1993]. Indeed, a recent physiological study, using stimuli similar to those used in present study, revealed that many neurons in the monkey's V1 respond to both first- and second-order motion [Bourne et al., 2002]. The second-order motion used in that study was the motion of a square area defined by coherent motion against a background of dynamic texture. One can easily assume that such cue-invariant neurons would respond to the motion of an object defined by both first- and second-order attributes and are involved in the interaction of the two neural pathways.

The existence of second-order attributes affecting first-order motion processing, as seen in the response to AMx, indicates collateral input from the second-order motion detection pathway to the first-order pathway. This corresponds well to the collateral implementation model, which has been proposed to explain the results of psychophysical studies with motion-defined motions [Zanker and Burns, 2001]. This model has two distinct pathways: one is a fine-grain network for primary motion information and the other is a coarse-grain network for secondary motion information. The former, which has a higher spatial resolution, is processed after spatial integration in the latter network. This feature, which is unique to this model, explains well the response properties of AMx.

The results of the present study corroborate the view that the extrastriate area, MT or V5, is the cardinal structure for the perception of cue-invariant motion [Albright, 1992]. That is, the

cortical sources of the first responses to both first- and second-order motion, despite having response latencies that differ by 100 msec, were estimated to lie near the upper limb of the inferior temporal sulcus (Fig. 5), which has been proposed to be the anatomical location of the human homologue of MT/V5 [Dumoulin et al., 2000; Watson et al., 1993]. This result was reproduced with the whole-head MEG system (Fig. 6). Previous fMRI studies also revealed that various second-order motions activated MT+ to the same magnitude as did the first-order motions [Seiffert et al., 2003; Smith et al., 1998]. In contrast, the results of single-neuron activity measurements in MT/V5 and V1 are inconsistent. The reported percentage of cue-invariant neurons in MT/V5 varies from 25% [O'Keefe and Movshon, 1998] to 87% [Albright, 1992]. Furthermore, no neurons in MT and MST respond explicitly to theta motion [Churan and Ilg, 2001]. Considering that detectable MEG responses originate mainly from synchronized excitatory inputs to the millions of pyramidal neurons in a localized cortical region [Hamalainen et al., 1993; Okada et al., 1997], neural correlates of uniform motion information may be represented in the population activity of the extrastriate areas more explicitly than it is in single-neuron activity, as demonstrated by fMRI studies.

It is possible that both first- and second-order motion are processed independently of each other, and that the two neural pathways exist in different cortical areas, as suggested by various human case studies [Vaina et al., 1999, 2000; Vaina and Cowey, 1996]. Substantial overlap in the cortical areas, however, has also been shown [Greenlee and Smith, 1997]. Whereas one fMRI study [Smith et al., 1998] has demonstrated a subtle but significant difference in the distribution of the cortical areas that respond to first- and second-order motion, a more recent fMRI study revealed no difference in the cortical activation patterns elicited by the two types of motion [Seiffert et al., 2003]. The subcortical extent of the lesions in patients' brains can also alter the type and magnitude of observed deficits, even though similar cortical areas were involved. Further imaging studies with various second-order motion types may elucidate the functional localization of the uniform neural pathways underlying second-order motion processing.

CONCLUSION

Using motion-defined motion stimuli, we demonstrated a distinct difference in the human cortical responses to first- and second-order motions and showed that an interaction exists between the two motion-processing pathways. The estimated cortical sources of the magnetic responses to these stimuli corresponded anatomically to MT+ for both first- and second-order motion. The characteristics of the interaction observed in this study correspond well to the collateral implementation model [Zanker and Burns, 2001]. Our study shows that non-invasive study with MEG can elucidate a complex neural process underlying the perception of higher-order motion, although further study is necessary to determine the extent to which the present results can be generalized.

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