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Short communication

Cortical responses to object-motion and visually-induced self-motion perception

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Abstract

We investigated the spatiotemporal cortical dynamics during the perception of object-motion and visually-induced self-motion perception in six normal subjects, using a 143-channel neuromagnetometer. Object-motion specific tasks evoked early transient activity over the right temporooccipital cortex, while self-motion perception, or vection, additionally was followed by sustained bilateral activity in the temporoparietal area. The specific signal distributions suggest to represent the different perceptual modes of object-motion and self-motion sensation. © 2001 Elsevier Science B.V. All rights reserved.

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When a visual scene is set into motion, the brain has to make a decision between two possible interpretations: either the world or the observer is moving. During vection, the observer perceives the moving stimulus as being stable, inducing a compelling sense of self-motion, as experienced in a stationary train, when the train alongside starts moving away. Cortical visual–vestibular interaction is thought to account for this illusion [8]. In terms of object-motion, several neuroimaging studies have defined motion-related cortical areas in humans [10,12,19]. Comparatively much less is known about the neuronal substrates of visuallyinduced perception of self-motion. In the present study we used magnetoencephalography (MEG) to compare the cortical dynamics of object-motion and visually-induced apparent self-motion perception.

The stimulus consisted of black and white bars (width 3 cm), generated by a PC-compatible software (ERST-VIPL, BeriSoft Corp.). The signal was fed into a video projector,

which projected the stimulus via a mirror onto a tangent screen inside the shielded room. The pattern moved with a velocity of 4.9°/s at a viewing distance of 150 cm and the test field subtended $50^{\circ} \times 32^{\circ}$. The subjects fixated binocularly a central fixation dot during each motion stimulation task. In the object-motion task, after a 2-s period during which subjects observed a stable pattern, the pattern started to move randomly either leftward or rightward for 2 s. In the self-motion task, subjects were exposed to the same moving pattern for 10 s, followed by motion reversal. All subjects underwent several training sessions, so that all experienced vection within 5-10 s after stimulation onset. As the onset of self-motion sensation could neither be externally triggered nor be indicated by the subject during the recording, we used the technique of motion reversal while the subjects experienced vection in order to assess self-motion specific cortical responses.

Head motion impulses are the most specific stimuli to induce short latency vestibular evoked potentials [11]. In analogy to these vestibular potentials, visual motion reversal during vection sensation represents an adequate trigger for the assessment of cortical responses during visual–

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vestibular interaction. All subjects reported a compelling sensation of self-motion during prolonged visual motion stimulation and during motion reversal.

Six healthy right-handed adults (mean age 29.2 years; range 24-35, two females), participated in the study. The experiments were undertaken with the understanding and written consent of each subject. Neuromagnetic activity was recorded using a whole-head MEG (CTF[™] Systems Inc., Canada) with 143 planar SQUID (Superconducting Quantum Interference Device) gradiometers at a sampling rate of 250 samples/s. Eye fixation stability was monitored by electrooculography. Indicator coils were attached to each subject's head, allowing precise superposition of the MEG sources onto MR images. Approximately 40 responses were averaged online in each stimulus category, in 2.5-s time window with a 500-ms prestimulus baseline. Data recording was triggered by the grating motion onset in the object motion task and by motion reversal in the self-motion task. In each subject head MRI was performed using a 1.5-T Siemens Vision system. The averaged evoked responses were digitally lowpass filtered at 0.5-10 Hz off line. The equivalent current dipole (ECD) model was used to determine the location of the magnetic fields. The dipoles were introduced into a time-varying multidipole model, enabling the dipole strengths to vary in a defined time window and allowing a comparison of field strengths between distinct cortical areas as a function of time. The goodness-of-fit (g) of the model was used to describe the proportion of the measured field variance explained by the calculated ECD. Only ECDs with a g value larger than 80% were accepted. The mean and standard deviation (S.D.) of the distance between the mean and each subject's dipole location was calculated to obtain the 95% confidence radius (=mean±2 S.D. of the distance).

The magnetic field evoked by motion onset consisted of a single transient component with a distinct dipolar field in all subjects (peak latencies: 200 to 240 ms, 95% confidence radius: 0.5 to 22 mm, Fig. 1a). This transient was found to be consistent across all subjects, and all components clustered within the right occipitotemporal area. MRI correlation provided a localization of three transients in the area corresponding to the human homologue of monkey middle temporal area (MT, or V5) and of one in the medial superior temporal area (MST). Two components were localized more dorsally but clearly outside the primary visual cortex, in the right extrastriate area. Fig. 2a shows the location of the dipole for subject 6 in the right occipitotemporal area. Reversal of the direction of motion while subjects perceived self-motion evoked a transient response which was followed by a sustained signal in all subjects. The transient responses were clustered in the right occipitotemporal area (peak latencies: 190 to 260 ms, 95% confidence radius: 0.3 to 28 mm, Fig. 1b). In four subjects the location of the transient would also correspond to the human homologue of monkey middle temporal area

(MT, Fig. 2b). One dipole was located more medially to MT and one was in the right postcentral gyrus.

The transient component was followed by a bilateral sustained field component, pronounced on the right hemisphere (Fig. 1c and d). This activity was sustained in the sense that it provoked several peaks with similar spatial distribution (peak latencies: 570 to 810 ms, 95% confidence radius: 0.8 to 13 mm on the right hemisphere, and 1 to 41 mm on the left). All dipoles clustered in the temporoparietal area (Fig. 2c and d). In the right hemisphere, the dipoles of four subjects could be clearly localized in the inferior parietal lobule, while two components were found in the temporoparietal borderzone. On the left side, four dipoles were within the inferior parietal lobule, one was within the middle temporal area, and one was between the supramarginal and parietal gyrus.

The principal finding of our study is the different spatiotemporal pattern of the major source activities in the object-motion and the self-motion condition. The latency and location of the transient following motion onset was within the range found in previous studies [10,16,18,19]. In four of our subjects the location of the dipoles would be consistent with activity in the human homologue of MT and MST. Wide-field motion stimulation results in activation of extrastriate cortical areas in addition to MT and MST, which may account for the dipoles found within the extrastriate cortex in two of our subjects [6]. A striking feature in all our subjects was the finding that the dipoles were restricted to the right occipitotemporal cortex. Although other investigators have reported bilateral activation [19], several imaging studies found strict unilateral activation of the right occipitotemporal area in motion stimulation [6,9,10].

Involvement of area MT (V5) in the processing of motion reversal has been shown in previous reports [1,12], but it has been argued that it seems unable to generate a strong enough regional cerebral blood flow change to be detected by PET [7]. Electro- and psychophysiological experiments suggest that perception of self-motion involves activation of the vestibular cortex [5,13,17]. However, recent PET findings could not demonstrate any cortical vestibular activity during vection illusion. Instead, bilateral activation of the medial parietooccipital area has been reported [3].

We found a consistent and sustained bilateral activation in the temporoparietal area in all subjects during selfmotion perception, being spatiotemporally distinct from both motion onset and motion reversal transients. In four subjects localization of the dipoles within the inferior parietal lobule could be demonstrated. Our findings correlate with previous imaging studies [2,4]. In these reports, the temporoparietal cortex, including the inferior parietal lobule, was found to be a part of the central vestibular system. In particular, spatial disorientation caused by vestibular stimulation activated these cortical areas. In our study spatial disorientation was induced visually by motion



Fig. 1. Magnetic field maps of subject 6. Magnetic field distributions are shown for motion onset (a) and for motion reversal (early transient responses (b), and bilateral sustained responses (c, d)). The time courses of magnetic field changes at the sensors MRP42 (a, b), MLP23 (c) and MRP23 (d) are also displayed.

reversal during self-motion perception. The suggestion that the temporoparietal cortex, especially the inferior parietal lobule is essential for visual–vestibular interaction is supported by the fact that visual–vestibular neurons were found in the posterolateral part of the inferior parietal lobule [14,15].

The sustained activity in the self-motion task, which can be interpreted as recurrent dipoles with similar spatial distribution, suggests that vection might be related to the cyclical involvement of a given neural network. The position of area MT or V5 can vary by as much as several centimetres as shown in a study combining PET and MRI [19], which was also confirmed by MEG findings [16]. This interindividual variability was also present in our study, and may be attributable to the variability of the sulci in human cortex. The findings in the motion reversal task during selfmotion perception imply two aspects of processing in visual-vestibular interaction and circular vection. The initial phasic process in area MT seems to represent basic detection of changes in the direction of motion. The sustained activity in the temporoparietal cortex, particularly in the inferior parietal lobule, could correspond to processing of self-motion perception and reorientation, reflecting input from multisensory vestibular areas and interactive processes over time.

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Fig. 2. Location of the dipoles for subject 6 for each task are overlaid onto MRI sections in the coronal, axial and sagittal plane. Motion onset (a) and transient motion reversal dipoles (b) are located in the right temporooccipital junction, whereas dipoles for the sustained activity during self-motion perception and motion reversal are located in the left (c) and right (d) temporoparietal area.

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