NeuroImage

www.elsevier.com/locate/ynimg
NeuroImage 21 (2004) 593–600

Neuromagnetic activity in medial parietooccipital cortex reflects the perception of visual motion during eye movements

Alexander Tikhonov,[a] Thomas Haarmeier,[a,b,*] Peter Thier,[a] Christoph Braun,[c] and Werner Lutzenberger[c]

[a] *Department of Cognitive Neurology, University of Tübingen, D-72076 Tübingen, Germany*
[b] *Department of General Neurology, Hertie-Institute for Clinical Brain Research, University of Tübingen, D-72076 Tübingen, Germany*
[c] *Institute of Medical Psychology and Behavioural Neurobiology, University of Tübingen, D-72076 Tübingen, Germany*

Received 27 May 2003; revised 17 September 2003; accepted 17 September 2003

We usually perceive a stationary, stable world despite coherent visual motion induced by eye movements. This astonishing example of perceptual invariance results from a comparison of visual information with internal reference signals (nonretinal signals) predicting the visual consequences of an eye movement. The important consequence of this concept is that our subjective percept of visual motion reflects the outcome of this comparison rather than retinal image slip. To localize the cortical networks underlying this comparison, we compared magnetoencephalography (MEG) responses under two conditions of pursuit-induced retinal image motion, which were identical physically but—due to different calibrational states of the nonretinal signal prompted under our experimental conditions—gave rise to different percepts of visual motion. This approach allows us to demonstrate that our perception of self-induced visual motion resides in comparably "late" parts of the cortical hierarchy of motion processing sparing the early stages up to cortical area MT/V5 but including cortex in and around the medial aspect of the parietooccipital cortex as one of its core elements.

Keywords: Eye movements; Neuromagnetic activity; Parietooccipital cortex

Introduction

To maintain a sense of perceptual spatial stability despite ego motion is one of the most important prerequisites for successful spatial orientation. Towards this end, the brain has to discriminate sensory signals resulting from the observer's own activities from those arising from the external world. Eye movements such as smooth pursuit eye movements may serve as a case in point. They allow us to stabilize the image of a selected object on or close to the fovea to make use of the advantages offered by foveal vision (Haarmeier and Thier, 1999). The inevitable consequence is that the images of all other objects (the "visual background") will, if stationary in the world, move on the retina at a speed equal to the speed of the pursuit eye movement carried out, however, without being perceived as moving. Building on early suggestions by von Helmholtz (1962) and supported by extensive psychophysical work (Haarmeier and Thier, 1996; Haarmeier et al., 1997, 2001; Wertheim, 1994), it is commonly believed that our visual system uses an internal reference signal predicting the visual consequences of the eye movement to perceptually erase retinal image motion resulting from smooth pursuit. Specifically, this inferential theory of perception (von Holst and Mittelstaedt, 1950; Wertheim, 1994) holds that background motion is perceived only if actual image motion on the retina deviates from its prediction.

The reference signal, optimally predicting the sensory consequences of the eye movement, cannot be a simple replica of the eye movement motor command. Rather it has to take the spatial and temporal composition of the visual world, captured by variables such as frequency content, luminance, or contrast into account. Since this composition changes continuously, also the reference signal must change, even though the eye movement motor command may be the same (Haarmeier et al., 2001). In the laboratory, insufficiencies of the reference signal, prompting a compensatory recalibration, can be induced by stimulating the visual system with visual motion, deviating from the visual motion expected from the pursuit eye movement carried out (Haarmeier et al., 2001). We here exploited this possibility to change the size of the reference signal and thereby the percept of visual motion to delineate the cortical substrate underlying the inferential mechanism using magnetoencephalography (MEG).

Specifically, we recorded neuromagnetic responses under two conditions of pursuit-induced retinal image motion, which were identical physically but—due to the reference signal being different under these two conditions—gave rise to different percepts of background motion. This experimental approach allowed us to dissociate MEG responses reflecting the physical attributes of the stimulus from those reflecting differences in the size of the reference signal and thus differences in the perception of background motion.

---

* Corresponding author. Department of General Neurology, Hertie-Institute for Clinical Brain Research, University of Tübingen, Klinikum Schnarrenberg, Hoppe-Seyler-Straße 3, 72076 Tübingen, Germany. Fax: +49-7071-295326.
E-mail address: thomas.haarmeier@uni-tuebingen.de (T. Haarmeier).

1053-8119/$ - see front matter © 2003 Elsevier Inc. All rights reserved.
doi:10.1016/j.neuroimage.2003.09.045

Materials and methods

Visual stimulation and psychophysical procedure

MEG responses were collected from eight normal subjects who executed linear rightward smooth pursuit eye movements across a stationary background stimulus, a random dot pattern of low contrast briefly presented while the eyes were close to straight ahead (Experiment 1; Fig. 1A) (Haarmeier and Thier, 1998). Stimuli were rear projected onto a large translucent screen (frame rate 60 Hz, 800 × 600 pixel) positioned at a viewing distance of 92 cm in the magnetically shielded room. Viewing was binocular. A red dot (diameter 10 min of arc) served as the pursuit target, which was presented for 0.5 s in the middle of the screen at the beginning of each trial. In Experiment 1 (rightward pursuit), the target next jumped 15° to the left and then moved to the right at a constant velocity of 10°/s spanning a visual angle of 30° (step-ramp paradigm). Temporally in the middle of the target sweep, the background pattern was presented for 360 ms. The background stimulus subtended 60° × 52° of visual angle and consisted of 350 white dots (diameter 15 min arc, luminance 65 cd/m^2) plotted in front of a dark background. Subjects were required to track the pursuit target as accurately as possible and to indicate at the end of each trial whether they had seen the background moving to the right or to the left (two alternative forced choice). To exactly quantify the background motion perceived during “MEG trials” (120 trials; background always stationary), we determined the velocity of external horizontal background motion required to yield the percept of a stationary background. To this end, a second type of trials (“PEST trials”) was presented randomly interleaved with MEG trials. They consisted of coherent horizontal background motion whose velocity was varied by an adaptive staircase procedure (Fig. 1B), converging on a point of subjective stationarity (PSS). At the PSS on average, as many left as right responses are given (Fig. 1C) because the retinal image motion signal matches the internal reference signal and the two cancel each other. Hence, the retinal

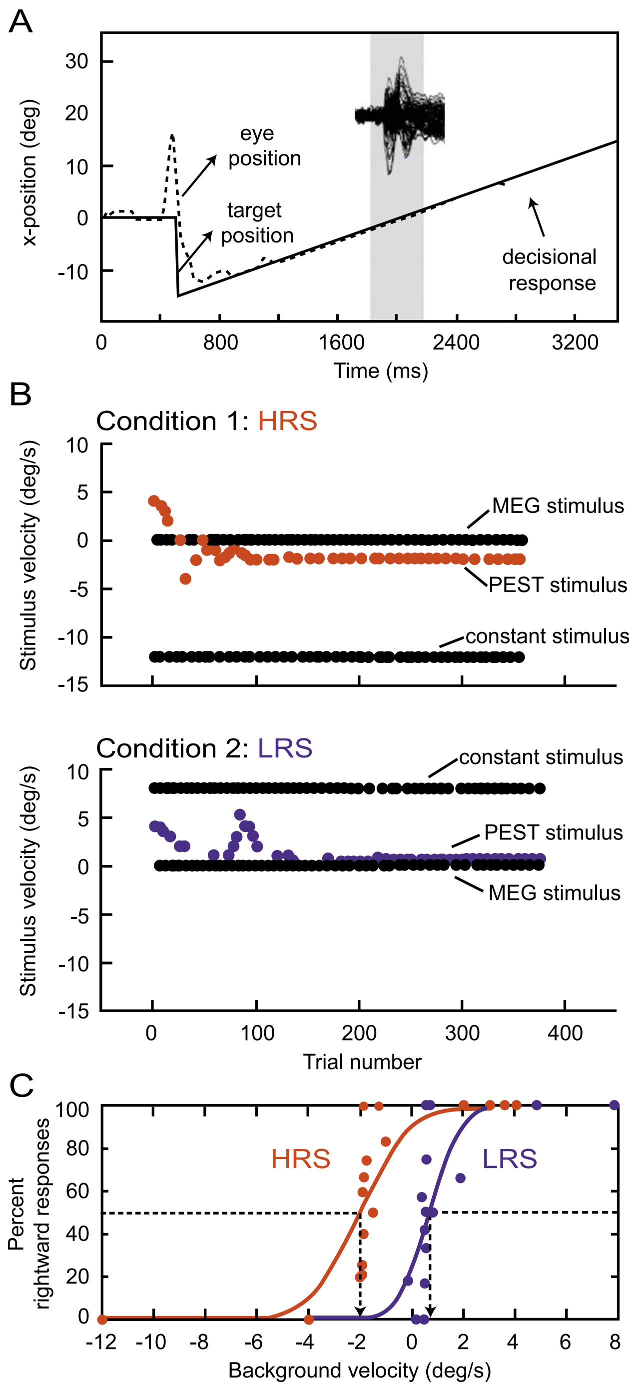


Fig. 1. Psychophysical paradigm and exemplary results of a single subject. (A) Time course of an MEG trial. The subject performs smooth pursuit eye movements elicited by a small dot moving at 10°/s to the right. While the eyes are close to straight ahead, a stationary random dot background is presented for 360 ms (duration indicated by grey column). The subject is instructed to maintain pursuit and to report the direction of perceived background motion by pressing one of two alternative keys. Inset: neuromagnetic recordings elicited by the presentation of the background stimulus. (B) Example of temporal sequence of stimulus velocities presented to one of the subjects under the two experimental conditions. Each dot marks one trial. Negative background velocities indicate direction opposite to eye movements. MEG stimuli, PEST stimuli, and constant stimuli all presented during pursuit to the right serve different purposes. Under both conditions, MEG responses are only collected when a stationary background is presented. PEST trials follow an adaptive staircase procedure converging towards the point of subjective stationarity (PSS), thus yielding a quantitative measure of the motion perceived during MEG trials. Constant trials with high background velocity in either the same (Condition 2; lower panel) or opposite (Condition 1; upper panel) direction to eye movements induce large discrepancies between the pursuit velocity and the size of the retinal image motion and initiate changes of the pursuit associated reference signal as reflected by different endpoints of the adaptive staircase procedure. (C) Percentage of “rightward” responses of the exemplary subject as function of the velocity of the background stimulus (all stimulus classes). The turning point of the probit functions fitted marks the physical background velocity at the PSS leading to as many right as left responses (dotted lines). Positive stimulus velocities at the PSS indicate that the background stimulus had to move in the same direction as the eyes, thereby reducing the retinal image motion received to cause the sensation of stationarity and thus signify a low reference signal (LRS condition). Conversely, negative stimulus velocities indicate enlarged retinal image motion and reference signal (HRS condition). Because the physical background velocity needed to allow the percept of stationarity is equal in magnitude and opposite in direction to the motion perceived during pursuit across a stationary stimulus, the difference in PSS between conditions is a measure of the difference in the perception of motion during MEG trials.

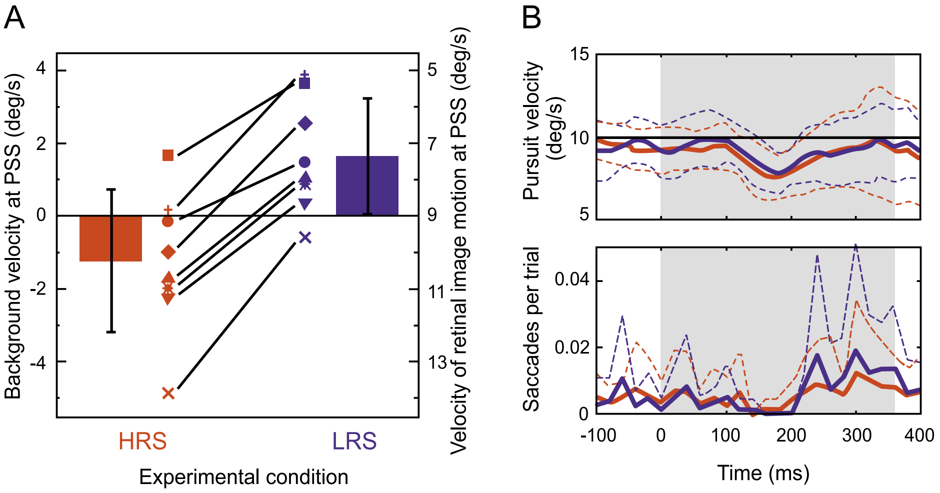


Fig. 2. Psychophysical and oculomotor results. (A) Stimulus velocity at the point of subjective stationarity (PSS) for the HRS and LRS conditions (eight subjects, represented by individual symbols and means/standard deviations). The size of the pursuit-related reference signal can be deduced from the right *y*-axis, which gives the velocity of the retinal image velocity at the PSS being the difference between measured pursuit velocity (which averaged 9°/s) and background velocity at the PSS. Positive stimulus velocities at the PSS (left *y*-axis) indicate that the background stimulus had to move in the same direction as the eyes, thereby reducing the retinal image velocity (right *y*-axis) to cause the sensation of stationarity and thus signify low reference signals. Conversely, negative stimulus velocities at PSS denote large reference signals. (B) Means and standard deviations of pursuit velocity (eight subjects; upper panel) and frequency of saccades (lower panel) during MEG trials given for a 500-ms time window starting 100 ms before background stimulus presentation (grey area).

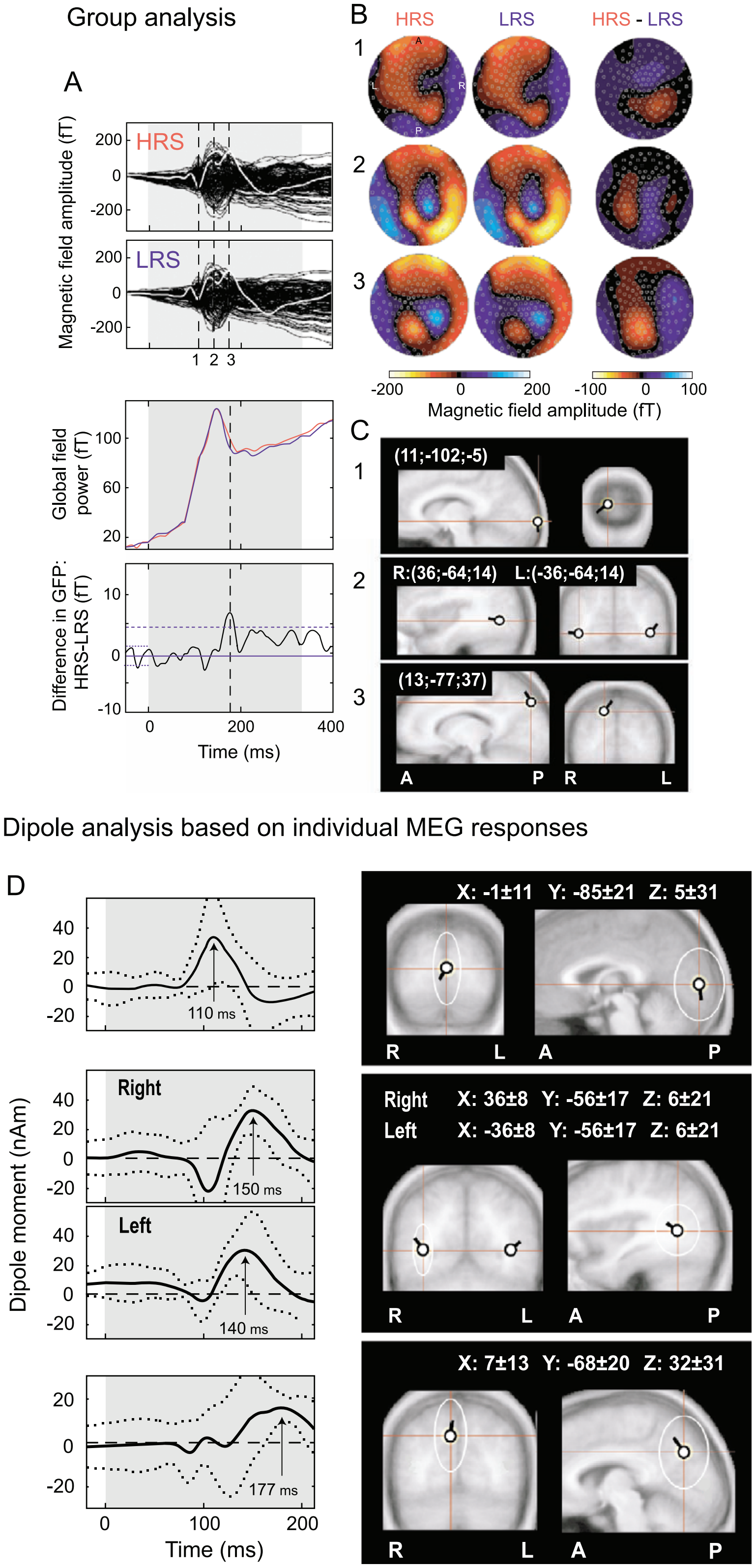
image velocity at the PSS is equal but opposite to the direction of the reference signal and thus provides an operational measure of the latter. Moreover, the background stimulus velocity needed to allow the percept of stationarity is equal in magnitude but opposite in direction to the motion (erroneously) perceived during pursuit across a physically stationary stimulus, thus giving a quantitative measure of the motion perceived during MEG trials (Haarmeier and Thier, 1996, 1998; Haarmeier et al., 1997, 2001; Mack and Herman, 1973; Wertheim, 1994). While MEG stimuli were used to collect neuromagnetic responses and PEST stimuli to measure the background motion perceived, a third stimulus class, presented randomly interleaved with the two previous ones, was designed to create two perceptually distinct conditions by changing the reference signal predictably. These “constant trials” consisted of smooth pursuit across backgrounds moving at a high constant velocity either in the direction (Condition 2; +8°/s; Fig. 1B, lower panel) or opposite to the direction (Condition 1; −12°/s; Fig. 1B, upper panel) of the eyes. We have recently shown that our visual system assumes that the percept of background motion repeatedly evoked in these constant trials is not due to external motion but due to an insufficient size of the reference signal and tries to adjust the reference signal accordingly, increasing it in Condition 1 and decreasing it in Condition 2 (Haarmeier et al., 2001). These compensatory changes of the reference signal, which have been shown to be prompted by a recalibration process directed to minimize the perception of background motion during pursuit (Haarmeier et al., 2001), become apparent as changes of the PSS (Haarmeier and Thier, 1998; Haarmeier et al., 2001) and are shown for a representative observer with the adaptive staircase procedure (PEST trials; Fig. 1B) converging towards different endpoints and two disparate psychometrical curves (Fig. 1C) for the two conditions. In accordance with our earlier observations (Haarmeier and Thier, 1996, 1998; Haarmeier et al., 2001), a closer look at the indices of the PSS for the two conditions (Fig. 1C) reveals that the reference signal changed in a way reducing the perception of movement of the background in constant trials. Since this was based on an increase of the reference signal in Condition 1, simulating a too-small reference signal in constant trials, and a decrease of the reference signal in Condition 2, simulating a too-large reference signal in constant trials, we will from now on refer to the two conditions as the “high reference signal” (HRS) and the “low reference signal” (LRS) conditions, respectively.

MEG, PEST, and constant trials were presented randomly interleaved with the probability of each trial being 0.33 (see Table 1 for a summary of the different classes of trials and their purposes). A single measurement was finished after 120 MEG trials excluding trials with artefacts. Each subject (n = 8; 2 of the experimentators, 6 naive) participated in two consecutive measurements differing only in the velocity of the constant trials. The sequence of these two measurements was randomized. The same

Table 1
Summary of the different classes of trials

Class of experimental trial	Background velocity (°/s)		Purpose
	Condition 1 (HRS condition)	Condition 2 (LRS condition)	
MEG trials	0 (stationary)	0 (stationary)	MEG recording
PEST trials	Determined by a staircase procedure	Determined by a staircase procedure	Measurement of the percept
Constant trials	−12 (opposite to eye movements)	+8 (same direction as eye movements)	Modification of the reference signal and the percept

paradigm was applied in Experiment 2 (leftward pursuit; nine subjects: two of the experimentators, seven naive) with minor differences, reflecting technical constraints concerning the pursuit velocity (10.8°/s) and the presentation of the background stimulus (380 ms). As the main perceptual measure, the PSS was defined as the background stimulus velocity that resulted in 50% right and 50% left responses after repeated presentations. It was determined by a probit analysis (McKee et al., 1982) with subsequent chi-square goodness-of-fit tests performed on the responses obtained for all three types of trials.



Recording of eye movements

Subjects were instructed to track the pursuit target as accurately as possible while avoiding head movements. Head movements were further reduced by usage of a bite bar attached to the MEG chair. During all experiments, eye movements were monitored using a homemade video system taking the pupil's center as measure of eye position. Recordings were stored at a sampling rate of 50 Hz on a SGI workstation synchronized with a second workstation, which generated the visual stimuli. The means of eye velocity and the frequency of saccades during background presentation were calculated off-line for each individual subject for the different classes of trials.

MEG recording and data analysis

MEG was recorded using a whole-head 151-channel MEG system (CTF Systems, Vancouver, Canada). Signals were low-pass filtered (cut-off frequency 100 Hz) and digitized at a sampling rate of 625 Hz. The trigger pulse started sampling at the presentation of the stationary fixation point. The total sampling epoch per trial was 3000 ms. MEG responses of 120 trials were averaged for each subject, digitally low-pass filtered at 40 Hz and baseline corrected with respect to the 100-ms interval preceding background onset.

Statistical analysis of the MEG responses was based on averages for individual subjects, calculated for each sensor and independently for the HRS and the LRS condition, respectively. Based on these averages, the global field power (GFP) was calculated for each of the two conditions as the root of the mean squared magnetic fields of all 151 sensors for each sample. To determine the temporal intervals, which showed significant differences of the MEG responses between conditions, we next compared the group mean differences in GFPs between the HRS and the LRS condition present after stimulus onset with the differences in GFPs obtained for an interval 200 ms before background onset. Specifically, a difference in mean GFP after stimulus onset was considered statistically significant if it surpassed a level defined by the mean difference in GFP plus three standard deviations derived from the 200-ms prestimulus interval.

The MEG responses were modeled as single equivalent current dipoles (ECD) whose three-dimensional locations and orientations were estimated by applying the analysis to the grand averages obtained for the HRS and LRS conditions, separately, for Experiments 1 and 2. Each of the four grand averages revealed three major first components, which were modeled at their peak latencies. The corresponding ECDs were determined by a least-square minimization procedure and based on a representative individual spherical head model, derived from anatomic magnetic resonance images (MRI) of one of the subjects. The first ECD corresponding to the time of the peak of the first visually evoked response was observed at 110 ms, the second one corresponded to the time of the second visually evoked response at 135 ms for leftward pursuit and 140 ms for rightward pursuit. The third one was the sample for which the GFP measures for the HRS and the LRS conditions yielded the largest significant difference (leftward pursuit: 160 ms, rightward pursuit: 175 ms). We modeled the neuromagnetic activity with the minimal number of the ECD required. In general, we used either two symmetrical ECDs (at 135 to 140 ms) or a single ECD (at 110 ms, at 160 ms after stimulus onset for leftward pursuit or at 175 ms for rightward pursuit) to model neuromagnetic activity arising from visual cortex depending on the magnetic field pattern. We accepted only ECDs accounting for >80% of the field variance of the whole sensor array (151 sensors) at the selected point in time. Before dipole fitting, frontal artefacts induced by the pursuit eye movements were eliminated by a subtraction of an estimate of the eye movement, obtained by low-pass filtering (0.625 Hz) the individual MEG averages.

To validate the ECD models derived from the grand averages, the neuromagnetic activity was also modeled by individual subjects. In this second analysis, applied to Experiment 1 (HRS condition) only, the MEG responses were modeled not for single points in time (peak latencies) but for a period of time ranging from 50 ms before to 250 ms after stimulus onset, using a 4-dipole approach (one pair of symmetric dipoles, two nonsymmetric ones) as suggested by the results of the ECD analysis of the grand averages. The individual MEG responses observed in this interval could indeed be adequately modeled by four dipoles for each of the individual subjects. The strength of the four different ECDs

Fig. 3. Neuromagnetic responses obtained under the HRS and LRS condition. (A) Upper two panels: grand averages of evoked neuromagnetic responses (eight subjects, 151 sensors overlaid) as function of time shown for a 450-ms time window starting 50 ms before stimulus presentation (grey area). The responses consist of diverging baseline drifts reflecting the pursuit eye movements (frontal sensors) and visual components more clearly discernable for one of the parietooccipital sensors (white curves). The dashed vertical lines mark the peak latencies of the first three major components. Third panel: mean global field power (GFP) signals of the MEG responses, that is, the root mean square across the 151 channels, averaged over all subjects for the HRS condition (red) and the LRS condition (blue). Lowest panel: difference in GFP between conditions. A first significant difference clearly surpassing the noise level (dashed horizontal line defined by the mean plus three STD of the differences present in the 200-ms prestimulus interval) arises at approximately 170 ms after stimulus onset denoting the third visual component (dashed vertical line). (B) Magnetic field maps of the grand averages obtained under the HRS condition (left column) and the LRS condition (middle column) and of the difference between conditions (right column). Maps are shown for three different points in time (1, 2, 3) corresponding to the numbered vertical lines in A marking the first three major visual components. Note that the difference observed for the third component is restricted to parietooccipital sensors and, in particular, spares the frontal sensors showing eye movement artefacts. (C) Dipole locations in Talairach space for the three visual components (1, 2, 3; same conventions as in B) from the grand average data obtained under the HRS condition. Frontal activity mostly reflecting eye movement artefacts was eliminated as specified in the methods section. The remaining activity was modeled by either a single dipole (first and third component) or a pair of dipoles (second component), each model accounting for at least 80% of signal variance. The same dipole locations were observed for the LRS condition (not shown). L: left; R: right; A: anterior; P: posterior. (D) Results of dipole analysis based on the MEG responses of the individual subjects (HRS condition): Strength of the four ECDs as function of time (left column; means and means ± one standard deviation given by solid and dashed lines, respectively) and their locations in Talairach space (right column). Despite interindividual variability of dipole locations (standard deviations marked by ellipses), the different sources match the dipole solutions derived from the grand averages. The four different dipoles exhibit different time courses and orientations with the fourth dipole having its peak at that point in time at which differences in GFP are present. The variance of the magnetic field explained by the dipole model averaged 80 ± 6% for the time interval examined.

as function of time was estimated for the entire interval while keeping position and orientation of the dipoles constant. The positions of the four different ECDs observed in the individual subjects were adjusted to Talairach standard space, averaged and mapped on the averaged MRI images to estimate interindividual variability of ECD locations. The analysis of both grand averages and individual MEG responses was based on running standard BESA software.

Results

For the eight subjects participating in Experiment 1 (rightward pursuit), the difference between background velocity at the PSS in the two conditions averaged 2.9°/s (Fig. 2A) and proved to be statistically highly significant (paired t test, $P < 0.001$). Importantly, this perceptual difference was not paralleled by differences in oculomotor performance, which was monitored in all experiments using a custom-made CCD oculometer (50 Hz). As evident from Fig. 2B, both the mean pursuit velocity and the occurrence of saccades during MEG trials were not statistically significantly different for the two conditions (running paired t tests; $P > 0.05$). Moreover, the pursuit velocity showed the same temporal profile with a transient decrease in pursuit velocity starting approximately 120 ms after the presentation of the large background stimulus and likewise paralleled by a transient decrease in the frequency of (catch-up) saccades. In summary, the analysis of eye movements revealed no difference that would account for any differences in the MEG responses.

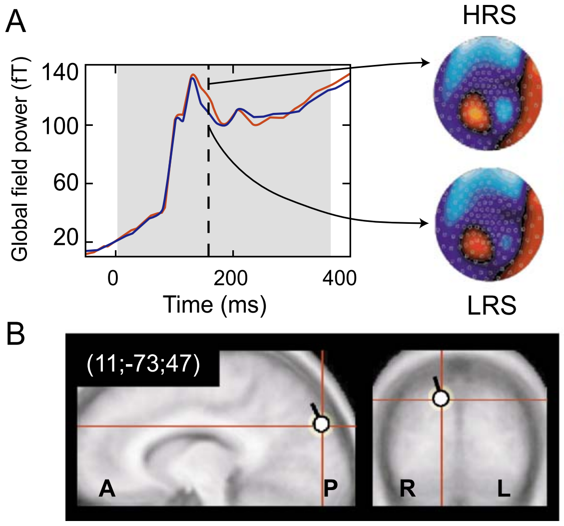


Fig. 4. Results of the second experiment testing the perception of visual motion during leftward pursuit. (A) Mean global field power (nine subjects) for the HRS condition (red) and the LRS condition (blue, same conventions as in Fig. 3A), magnetic field maps of the grand averages depicted for the component exhibiting significant differences between conditions (time point marked by the vertical dashed line), and (B) the corresponding dipole solution. Similar to the first experiment, differences in magnetic field size are confined to the third component following the largest visual peak and are located around medial parietooccipital cortex.

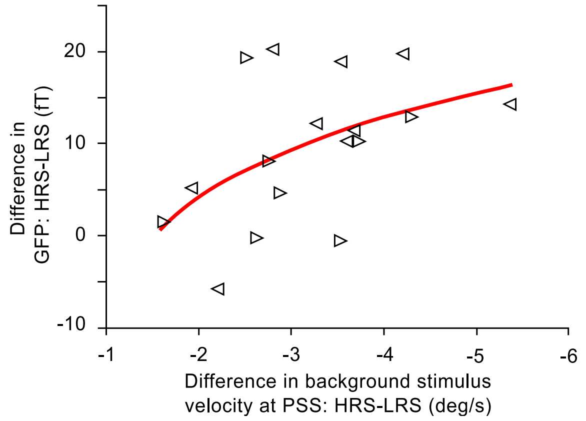


Fig. 5. Modulation of neuromagnetic activity as function of shift of the PSS. A change in neuromagnetic activity was captured by measuring a change in global field power at the time of the third component (166 to 188 ms for rightward pursuit, 144 to 168 ms for leftward pursuit). Individual symbols refer to individual subjects. The orientation of the triangles reflects the direction of pursuit (leftward [◁], rightward [▷]). Negative values on the x-axis denote larger retinal image velocities at PSS under the HRS condition as compared to the LRS. The relation between the individual change in motion perception and MEG modulation can be fitted significantly by a logarithmic function (red line; $y = 10.3 \times \ln(x - 0.49)$; $P < 0.05$).

As shown in Fig. 3A, the neuromagnetic responses obtained under the low and the high reference signal condition exhibited the same principal pattern of components for the two conditions, namely, low frequency baseline drifts reflecting the movement of the eye dipoles maximally influencing the frontal and inferior temporal sensors and more importantly visual components evoked by the pursuit-induced retinal image motion. The visual responses consisted of a series of transient deflections with a first major response at approximately 105 ms, a second component showing the largest amplitude (peak latency approximately 140 ms), followed by two further components with peak latencies at approximately 170 and 240 ms—a pattern and time course of activity that in principal was observed in all subjects. Exploiting the excellent temporal resolution offered by MEG recordings, we in a first step tried to determine at which latency the visual responses were different for the two conditions. As depicted in Fig. 3A, the statistical analysis of the difference in global field power between the two conditions (Fig. 3A, lower panel) revealed that the neuromagnetic responses did not differ, independent of the percept of motion, for more than 140 ms including the largest peak of the visual response observed at approximately 140 ms. First statistically significant differences were obtained some 170 ms after stimulus onset (13 consecutive samples exceeding the threshold defined by the mean plus three standard deviations of the differences in GFP present in the 200-ms interval preceding stimulus onset; 166 to 188 ms), denoting the latency of the third component of the sequence of visual responses having larger amplitudes for the HRS condition than for the LRS condition. The lack of significant differences of the early neuromagnetic responses on the one hand and the modulation of the third component on the other hand can also be drawn from Fig. 3B showing the field distribution of the neuromagnetic responses obtained under the two conditions. While the subtraction of the responses mutually erases any activity (including the frontal eye artifacts) observed until 140 ms after stimulus onset, significant activity centered around medial parietooccipital sensors survives subtraction at a latency of 175 ms. This result was reproduced in a second series of experiments in which the direction of pursuit was inversed. In this experiment, subjects (n = 9) performed leftward horizontal pursuit, again under the two conditions differing in the background motion perceived (difference in PSS between the HRS and LRS condition averaging 3.4°/s; $P < 0.001$) but being identical physically (leftward pursuit across a stationary background). As observed for rightward pursuit in Experiment 1, the earliest significant differences in the neuromagnetic responses were observed for the third component following the largest visual peak (Fig. 4A; 15 consecutive samples exceeding three standard deviations above noise level; 144 to 168 ms), again with larger neuromagnetic responses for the HRS condition. To assess in more detail the relation between the neuromagnetic activity and the percept of motion, we correlated the individual differences in GFP for the HRS and LRS conditions at the interval (time of third component) for which the group analysis had revealed significant differences with the individual change in motion perception as assessed by differences in the PSS. As can be drawn from Fig. 5, there was a significant correlation between the difference in neuromagnetic activity for the two perceptual conditions and the difference in the percepts with larger changes in neuromagnetic activity for larger shifts in motion perception.

In agreement with earlier MEG studies, localizing the responses to visual motion observed during stationary fixation (Anderson et al., 1996; Uusitalo et al., 1997; Vanni et al., 1997; Zeki et al., 1991), the first and second component of activation observed in our study could be adequately described by assuming a single equivalent current dipole close to the calcarine fissure (first component, Figs. 3C and D, upper two panels), reflecting an activation of early visual cortex such as areas V1 and V2, and by a pair of dipoles in left and right temporooccipital cortex (second component, Figs. 3C and D, middle row) exactly coinciding with area MT+/V5+ as delineated in numerous imaging studies (Previc et al., 2000; Watson et al., 1993). Different from this early visual activity unrelated to the perception of motion, the MEG component reflecting the change of the reference signal could be modeled by a single source in the medial parietooccipital sulcus (Fig. 3C) clearly distinct from the other active areas. Analysis of the grand averages revealed that this dipole was located slightly right off the hemispheric midline in both experiments (compare Fig. 4B), but analysis of subjects' individual MEG responses (Fig. 3D, lower two panels) suggested symmetrical activation of cortex around the hemispheric midline.

Discussion

Our study demonstrates that the inferential mechanism impeding self-induced motion to gain access to conscious perception involves medial parietooccipital (mPO) cortex. The early stages of cortical motion processing up to cortical area MT/V5, on the other hand, seem to be unable to distinguish whether visual motion is external or self-induced. Clearly, mPO cortex lies outside the classical dorsal stream of visual motion processing and we may ask why only a few imaging studies have found mPO cortex to be activated by visual motion at all. One possible answer is that mPO cortex may preferentially respond to large field visual motion as applied in only some of the more recent studies (Dukelow et al., 2001; Previc et al., 2000). In addition, a thorough characterization of the neuromagnetic activity attributed to mPO cortex by Portin et al. (1998) and Portin and Hari (1999), who presented stationary stimuli, has delineated several functional properties of this area making it well suited to serve the analysis of global field motion, that is, lack of retinotopy and of foveal magnification as well as low contrast dependency, the latter being a major feature of the visual motion processing pathway. The notion of a specific role in visual self-motion processing is also supported by the demonstration of PET activation in mPO cortex correlated with the perception of circular vection (Brandt et al., 1998). A second possible answer to the question why mPO cortex has not been consistently observed in imaging studies might be that its activity may primarily arise from the nonvisual reference signals needed for the ecologically correct interpretation of visual motion. However, these reference signals may be weak or even absent during passive viewing without eye movements as in most previous studies of motion perception.

Eye movements are one example of behavior influencing visual stimulation without distorting our perception of the external world. Another prominent example is eye blinks, which surprisingly do not infer with continuous vision, although they temporarily shut down retinal stimulation. Interestingly, there is evidence that mPO cortex may also be involved in ironing out the influence of this particular motor behavior on perception (Hari et al., 1994). Hence, medial parietooccipital cortex may be a part of cortex, essential for establishing a veridical percept of the external world and thereby contribute to the separation of self and nonself.

Acknowledgments

We thank the members of the Section on Experimental Magnetic Resonance Imaging of the Department of Neuroradiology, University of Tübingen, for their help with acquiring the anatomic MRI images. Supported by the DFG ("SPP 2001") and EC ARTESIMIT IST-2000-29689 project.

References

Anderson, S.J., Holliday, I.E., Singh, K.D., Harding, G.F., 1996. Localization and functional analysis of human cortical area V5 using magneto-encephalography. Proc. R. Soc. Lond. B. Biol. Sci. 263, 423–431.

Brandt, T., Bartenstein, P., Janek, A., Dieterich, M., 1998. Reciprocal inhibitory visual-vestibular interaction. Brain 121, 1749–1758.

Dukelow, S.P., DeSouza, J.F.X., Culham, J.C., van den Berg, A.V., Menon, R.S., Vilis, T., 2001. Distinguishing subregions of the human MT + complex using visual fields and pursuit eye movements. J. Neurophysiol. 86, 1991–2000.

Haarmeier, T., Thier, P., 1996. Modification of the Filehne illusion by conditioning visual stimuli. Vis. Res. 36, 741–750.

Haarmeier, T., Thier, P., 1998. An electrophysiological correlate of visual motion awareness in man. J. Cogn. Neurosci. 10, 464–471.

Haarmeier, T., Thier, P., 1999. Impaired analysis of moving objects due to deficient smooth pursuit eye movements. Brain 122, 1495–1505.

Haarmeier, T., Thier, P., Repnow, M., Petersen, D., 1997. False perception of motion in a patient who cannot compensate for eye movements. Nature 389, 849–852.

Haarmeier, T., Bunjes, F., Lindner, A., Berret, E., Thier, P., 2001. Optimizing visual motion perception during eye movements. Neuron 32, 527–535.

Hari, R., Salmelin, R., Tissari, S.O., Kajola, M., Virsu, V., 1994. Visual stability during eye blinks. Nature 367, 121–122.

Mack, A., Herman, E., 1973. Position constancy during pursuit eye movement: an investigation of the Filehne illusion. Q. J. Exp. Psychol. 25, 71–84.

McKee, S.P., Klein, S.A., Teller, D.Y., 1982. Statistical properties of forced choice psychometric functions: implication of probit analysis. Behav. Percept. Psychophysiol. 37, 286–298.

Portin, K., Hari, R., 1999. Human parieto-occipital visual cortex: lack of retinotopy and foveal magnification. Proc. R. Soc. Lond., B. 266, 981–985.

Portin, K., Salenius, S., Salmelin, R., Hari, R., 1998. Activation of the human occipital and parietal cortex by pattern and luminance stimuli: neuromagnetic measurements. Cereb. Cortex 8, 253–260.

Previc, F.H., Liotti, M., Blakemore, C., Beer, J., Fox, P., 2000. Functional imaging of brain areas involved in the processing of coherent and incoherent wide field-of-view visual motion. Exp. Brain Res. 131, 393–405.

Vanni, S., Uusitalo, M.A., Kiesila, P., Hari, R., 1997. Visual motion activates V5 in dyslexics. NeuroReport 8, 1939–1942.

von Helmholtz, H., 1962. Physiological Optics, vol. III. Dover, New York. Tr. from 3rd German ed. 1910.

von Holst, E., Mittelstaedt, H., 1950. Das Reafferenzprinzip. Naturwissenschaften 37, 464–476.

Watson, J.D., Myers, R., Frackowiak, R.S., Hajnal, J.V., Woods, R.P., Maziotta, J.C., Shipp, S., Zeki, S., 1993. Area V5 of the human brain: evidence from a combined study using positron emission tomography and magnetic resonance imaging. Cereb. Cortex 3, 79–94.

Wertheim, A.H., 1994. Motion perception during self-motion: the direct versus inferential controversy revisited. Behav. Brain Sci. 17, 293–355.

Uusitalo, M.A., Virsu, V., Salenius, S., Näsänen, R., Hari, R., 1997. Activation of human V5 complex and rolandic regions in association with moving visual stimuli. NeuroImage 5, 241–250.

Zeki, S., Watson, J.D., Lueck, C.J., Friston, K.J., Kennard, C., Frackowiak, R.S., 1991. A direct demonstration of functional specialization in human visual cortex. J. Neurosci. 11, 641–649.