

Selective Attention Increases the Dependency of Cortical Responses on Visual Motion Coherence in Man

Barbara Händel^{1,2}, Werner Lutzenberger³, Peter Thier² and Thomas Haarmeier^{1,2}

¹Department of General Neurology, ²Department of Cognitive Neurology, Hertie-Institute for Clinical Brain Research, and ³Institute of Medical Psychology and Behavioural Neurobiology, University of Tübingen, 72076 Tübingen, Germany

Attention improves visual discrimination and consequently allows to discern stimuli with low signal-to-noise ratios that otherwise would remain undetected. We used magnetoencephalography (MEG) to test whether neuromagnetic responses recorded from occipito-temporal cortex, reflecting the size of visual motion signals embedded in noise (motion coherence), would mirror the perceptual changes induced by attention. Attention directed to a given hemifield increased and decreased the coherence modulation of the MEG response over contralateral and ipsilateral visual cortex, respectively, indicating a change in the neuronal signal-to-noise ratio at the population level.

Keywords: delta oscillations, magnetoencephalography, signal-to-noise ratio, visual motion perception

Introduction

Selective visual attention is a mechanism that improves perception by selecting which signals receive further processing: information which arises from a particular region in the visual field or which shares a particular feature is enhanced and deviating information is suppressed. Psychophysical studies have provided evidence for both mechanisms, the 1st assigning preference to behaviorally relevant stimulus information (“signal enhancement”) and the 2nd attenuating the disturbing impact of distractors (“noise reduction”) (e.g., Posner 1980; Downing 1988; Cave and Kosslyn 1989; Lu and Doshier 1998; Yeshurun and Carrasco 1999; Golla et al. 2004). Likewise, functional imaging studies and single-cell recordings have demonstrated that neural responses to attended visual stimuli are enhanced relative to the same stimuli when unattended (e.g., Moran and Desimone 1985; Corbetta et al. 1990; Treue and Maunsell 1996) and that neural responses to unattended stimuli are attenuated when vision is engaged elsewhere (Rees et al. 1997; for reviews see Kastner and Pisk 2004; Reynolds and Chelazzi 2004; Treue and Martinez-Trujillo 2006).

A direct correspondence between psychophysical and neurophysiological measures has been carefully established by studies in awake behaving monkeys (e.g., Newsome et al. 1989; Britten et al. 1992; Cook and Maunsell 2002). Requiring the monkey to extract a global motion signal embedded in noise by varying the signal-to-noise ratio, that is, the percentage of coherently moving elements, psychometric and “neuro-metric” functions could be compared in a quantitative manner. Following this approach, numerous studies have revealed positive, approximately linear correlations between motion coherence and firing rate such as observed in area MT/V5 (Newsome et al. 1989; Britten et al. 1992, 1996) or area LIP

(Shadlen et al. 1996, 2001; Roitman and Shadlen 2002; Gold and Shadlen 2003). This correspondence reflects the simple rule that the discrimination of visual motion as predicted on the basis of neuronal responses of visual cortex will be better the more, the stronger and more reliably the responses would depend on motion coherence.

The goal of the present study was to test whether selective attention changes the dependency between cortical responses and motion coherence in accordance with its influences on perception. To this end, we resorted to a motion discrimination paradigm for which we recently observed a strong positive correlation between visual motion coherence and evoked neuromagnetic responses in man (Händel et al. 2007). Specifically, the magnetoencephalography (MEG) response examined was a low-frequency (3 Hz) oscillation, phase locked to stimulation and originating from contralateral extrastriate cortex (Händel et al. 2007). Similar to blood oxygenation level-dependent (BOLD) responses recorded from human extrastriate areas (MT+, V2, V3a: Rees et al. 2000; V3a: Braddick et al. 2001), evoked responses measured by electroencephalography (EEG) (Niedeggen and Wist 1999; Patzwahl and Zanker 2000) and MEG (Maruyama et al. 2002; Nakamura et al. 2003; Aspell et al. 2005) or high-frequency oscillations (Siegel et al. 2007), the amplitude of this response reflects a key feature of the response of motion-sensitive visual neurons, namely their coherence dependency, and was taken here as a compound measure of population responses in human extrastriate cortex. We report that selective attention has a profound influence on the coherence dependency of this oscillation, suggesting changes in the signal-to-noise ratio at the neural population level as predicted by single-cell recordings (Martinez-Trujillo and Treue 2004).

Materials and Methods

Seven healthy subjects, 2 males and 5 females with a mean age of 24 ± 3 years participated in this study. All subjects had normal or corrected to normal vision. Informed consent was obtained from all subjects according to the Declaration of Helsinki and the guidelines of the local ethics committee of the faculty of medicine of the University of Tübingen, which approved the study.

Psychophysical Task and Eye Movement Control

Subjects were seated upright in a magnetically shielded room (Vakuum-Schmelze, Hanau, Germany) and were instructed to sit as motionless as possible during the MEG recording. Stable posture was supported by a chinrest attached to the MEG chair. The computer-generated visual stimuli were rear projected onto a large translucent screen (DLP-projector, frame rate 60 Hz, 800×600 pixel, ~ 11 pixel per degree) positioned at a viewing distance of 92 cm in the magnetically shielded room. Viewing was binocular.

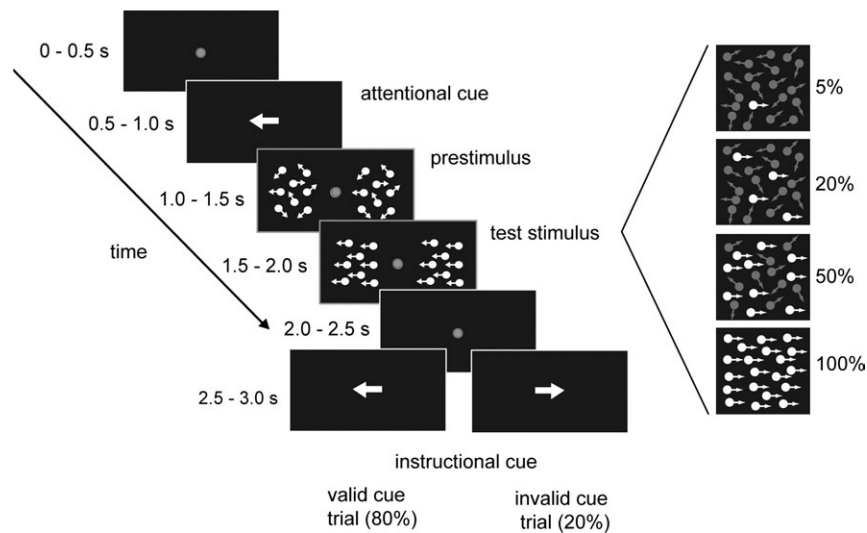


Figure 1. Experimental paradigm. The stimulus consisted of 6 periods each lasting 0.5 s. After a 1st fixation period an arrow instructed subjects to shift their attention either to the left or to the right. The 1st motion stimulus comprised 2 RDKs consisting of incoherent motion. The following test stimulus involved presentation of coherent motion defined by the percentage of dots moving in the same direction (5%, 20%, 50%, or 100%, stimulus schemata are shown on the right side). Global motion direction was either to the left or to the right and could be different for the 2 RDKs. After a subsequent 2nd fixation period, a 2nd arrow indicated for which of the 2 RDKs subjects had to indicate the direction of coherent motion (2-alternative forced choice). Valid cueing was applied in 80% of trials. Trials with predefined motion coherence (120 presentations each) served the collection of neuromagnetic responses and were presented randomly interleaved with trials whose motion coherence was varied according to an adaptive staircase procedure in order to determine the psychophysical thresholds.

The visual stimulus consisted of 6 periods, each lasting 500 ms (see Fig. 1). After a 1st fixation period (central fixation dot, diameter 10 arcmin) an arrow instructed subjects to covertly shift attention either to the left or the right hemifield. The attentional cue was followed by 2 random dot kinematograms (RDKs) each of which covered a square of $16 \times 16^\circ$ and was centered 15° right and left, respectively, of the fixation point. RDKs consisted of 1500 white squares (side length = 8 arcmin, lifetime = 1000 ms, dot density ~ 6 dots/deg², luminance 47 cd/m²) all moving incoherently, that is, in all possible directions with a resolution of 1° , at a common speed of 6 deg/s. After the presentation of this 1st pair of RDKs (“prestimulus”), a 2nd pair of RDKs, the “test stimulus,” started which would not induce visual responses related to luminance onset but was varied in such a way to induce responses depending on stimulus motion. The properties of the test stimulus were identical to those described for the prestimulus except that a certain percentage of the dot elements moved coherently in the same direction (either to the left or to the right). Specifically, the percentage of coherently moving dots was either 5%, 20%, 50%, or 100% of all dots in an individual trial. Although the amount of motion coherence was always identical for the 2 RDKs in a given trial, global motion direction could be the same or different as randomly chosen by the computer. After a subsequent 2nd fixation period, a 2nd arrow indicated for which of the 2 RDKs subjects had to indicate the direction of coherent motion (2-alternative forced choice). Valid cueing as defined by congruent orientation of the attentional and the instructional cue was applied in 80% of trials. Trials with a valid cue could either show predefined motion coherence (4 levels, 120 presentations each) or motion coherence varied according to an adaptive staircase procedure. Invalid cued trials showed only adaptive coherence levels. Only the valid trials with predefined motion coherence served the collection of neuromagnetic responses and were presented randomly interleaved with trials whose motion coherence was varied according to an adaptive staircase procedure in order to determine 2 psychophysical thresholds, 1 for the condition of valid cueing and a 2nd for the condition of invalid cueing. Start level of the procedure was 80% coherence which was increased (or decreased respectively) if 75% incorrect (or correct) trials (minimal sample size: 3 trials) were observed. This change started with a step of 20% and step size was halved in case the last change had caused convergence toward the 75% correct threshold, step size was doubled (if possible) in case the change had led further away from this threshold. The staircase

procedure was terminated (and started new) when the step size had reached a value of 0.02%.

In order to assess the ability to discriminate the motion direction embedded in noise, the percentage of correct responses was plotted as function of motion coherence and fitted by a probit function (McKee et al. 1985). The perceptual threshold was defined by the coherence level for which the probit function predicted 75% correct responses. In order to correlate perceptual discrimination with the electrophysiological responses obtained for the 4 coherence levels, the proportion of correct responses was derived also for these levels based on the same probit approximation and was then compared using paired *t* tests.

During all experiments, eye movements were monitored using a custom built video system taking the pupil’s center as measure of eye position. Recordings were stored at a sampling rate of 50 Hz and analyzed offline in order to assess the quality of fixation. In particular, the influence of spatial orienting on the following oculomotor parameters was tested for the period of test stimulus presentation, that is, deviations from the fixation point (eye position), and the number and amplitude of saccades. To this end, the means of the various oculomotor measures were calculated in each subject for the epoch of the test stimulus and compared between the 2 possible directions of the attentional cue by means of a paired *t*-test.

Recording and Analysis of the MEG Signals

Neuromagnetic activity was recorded using a whole-head MEG system (CTF, Inc., Vancouver, Canada). One hundred and fifty-one 1st-order axial magnetic gradiometers were used to collect the data which was analyzed without further interpolation. The signals were sampled at a rate of 625 Hz. Recording epochs lasted from stimulus onset to arrow offset plus 200 ms, leaving 3200 ms of recording time for each trial.

In order to test whether correlations between MEG responses and visual motion coherence and orientation of spatial attention might be confined to specific frequency bands, a spectral analysis of the unfiltered MEG signals was performed. This analysis was conducted on single trial basis in the range of 1–100 Hz (1.23 Hz bins) for 5 partially overlapping 700-ms time windows. The time windows were defined by the 6 different 500-ms epochs of stimulation (compare Fig. 1) each being expanded by the 100-ms interval immediately preceding and following, respectively, the individual epoch. The resulting recording points were reduced to 218 and zero-padded to obtain 256

points. To reduce the frequency leakage the records were multiplied by Welch windows as recommended by Press et al. (1992). A fast Fourier transform was calculated for each time window, each channel and each trial, separately. Then, spectral amplitudes (in the given time window) were averaged over all trials for each coherence level and each of the 2 conditions of attentional orienting (to the left or to the right) in each subject. The influence of motion coherence and attention on the spectral amplitudes was assessed by a 2-way analysis of variance performed on the unaveraged group of the 7 subjects and for each frequency band (1.23 Hz) and sensor ($n = 150$; 1 sensor was excluded because of malfunction), separately. Neighboring sensors showing P values of 2 adjacent frequency bins below 0.0018, calculated as $P = \sqrt{[0.05/(\text{number of channels} \times \text{number of frequency bins})]} = \sqrt{[0.05/(150 \times 100)]}$, were taken to be significant. Although no significant differences were observed for the 2 directions of attention, the influence of motion coherence was significant. Specifically, same as in our previous report (Händel et al. 2007) spectral power of 2 different frequency bands depended on motion coherence, that is, a low-frequency oscillation in the delta range (around 3 Hz) during test stimulus presentation and a 2nd in the alpha-frequency range (around 10 Hz) during the fixation period following the test stimulus. Only the low-frequency component showed significant dependencies on motion coherence for both directions of spatial orienting and also for corresponding sensors of both hemispheres. Thus, only the delta oscillation allowed for direct comparison of the 2 hemispheres further analysis was devoted to this response.

To this end, the recordings were 1st of all baseline (450–500 ms) corrected, Gaussian filtered (3 ± 2 Hz) for each trial and channel, and subjected to a Hilbert transformation (Lutzenberger et al. 2002) in order to extract the spectral amplitude which had been found previously to depend on motion coherence. Next, dependencies on motion coherence were tested for 2 separate datasets defined by the direction of spatial orienting in the given trial (to the right or to the left, respectively). To this end, for both conditions the amplitudes were averaged in each subject across the corresponding trials for each of the 4 different coherence levels, separately. The influence of motion coherence (5%, 20%, 50%, and 100%) on the spectral amplitudes was then assessed for both conditions by a 1-way repeated-measures analysis of variance (ANOVA) performed over all samples of the 7 subjects and for each channel ($n = 150$). This analysis was performed for 4 time periods of 250 ms starting from test stimulus onset till the offset of the 2nd fixation period. Sensors were considered to be significant if 2 neighboring sensors showed a P value below 0.05 in a given time period. Time periods showing significant sensors for both attentional states, that is, attention focused to the right or left hemifield, respectively, were further analyzed. Amplitudes of significant sensors during this time period were compared by means of a 3-way ANOVA with repeated measures with the factors motion coherence, hemisphere (location of sensors, either left or right) and sensor location relative to the attended hemifield.

Source Localization

The sources of the 3-Hz oscillation were localized by means of a beamformer algorithm. To this end, 3-dimensional imaging of brain activity was performed using synthetic aperture magnetometry (SAM; Robinson and Vrba 1999). SAM is a type of minimum variance beamformer which is sensitive for 4 dimensions (voxel location and source orientation) and therefore might result in a better spatial resolution as compared with conventional beamformers (for details see, e.g., Vrba and Robinson 2002). This specific type of minimum variance beamformer, implemented in the CTF software, was calculated for activity in the $3 (\pm 2)$ Hz frequency range. For a given subject a pseudo- t statistic was calculated to estimate the difference in source power between the period of coherent motion presentation (100% motion coherence, 1.5–2.0 s) and the 1st fixation period (0–0.5 s) at a given target voxel (voxel side length 1 cm; Robinson and Vrba 1999). This comparison was preferred to an alternative one testing the prestimulus (motion noise) versus the test stimulus (coherent noise) period because the latter would favor responses to motion noise due to stimulus onset. t values were plotted onto a head model derived from anatomic magnetic resonance images of 1 of the subjects which were

orthogonalized and normalized using the 152 subject T_1 -weighted average (ICBM 152) as template.

Results

Behavioral Results

Subjects shifted attention according to cue information as indicated by the fact that valid cueing resulted in perceptual thresholds of 19.9% (percentage of coherently moving dots required to obtain 75% correct responses) as opposed to 42.3% in trials with invalid cueing (t -test, $P < 0.01$, Fig. 2A). The strongest differences in perceptual discrimination were observed for intermediate coherence levels, i.e. for the 20% and 50% motion coherence stimuli (Fig. 2B). Specifically, group differences for the proportion of correct judgments were negligible for the 5% and 100% stimuli but amounted to 22.2% (20% coherence, t -test: $P < 0.005$, corrected for multiple comparisons by means of a Bonferroni correction) and 15.2% (50% coherence, not significant) for the other levels. As can be derived from Figure 2B, due to attentional instruction the behavioral performance at the 20% level with attention was very similar to the 1 possible without attention at the 50% level. Importantly, the perceptual modulation observed was not attributable to eye movements because all oculomotor parameters considered, that is, eye position and number and amplitude of saccades during presentation of the test stimulus, showed no significant difference between trials differing with respect to the direction of cueing (either to the left or to the right; paired t -test, $P > 0.05$ corrected for multiple comparisons). For instance, changes in horizontal eye position induced by the attentional cue were small amounting on average to only 0.4° (attention directed to the right: $+0.7^\circ \pm 0.3^\circ$ [means and SD]; attention directed to the left: $+0.3^\circ \pm 0.3^\circ$ [means and SD]).

Neuromagnetic Responses

As outlined in the Methods section, cortical responses were recorded during the task using whole-head MEG and analyzed off-line in order to search for dependencies on motion coherence and selective attention. Because our previous work had demonstrated a strong modulation of a 3-Hz oscillation by motion coherence the present analysis was focused on spectral amplitudes in a bandwidth of $3 (\pm 2)$ Hz (Händel et al. 2007). Corroborating our earlier finding, significant influences of motion coherence were strongest during the 2nd half of test stimulus presentation (250–500 ms after test stimulus onset). As shown in Figure 3B, which plots the grand averages, that is, averages over all subjects and all sensors, of the Gaussian filtered signal for the different coherence levels as function of time, this dependency was not strictly monotonic. The reason is that the amplitudes evoked by the 5% coherence stimulus were slightly higher relative to the 20% response thus deviating from the overall increase observed for higher coherence levels.

In order not to disregard nonmonotonic dependencies, we performed an analysis of variance not postulating a particular mathematical relationship. Specifically, dependencies on motion coherence and selective attention were tested by subjecting the spectral amplitudes derived from the 2nd half of the test stimulus period (250–500 ms after test stimulus onset) to a 1-way repeated-measures ANOVA with the factor motion coherence (4 levels) for the 2 directions of spatial orienting (to the left or to the right), separately. As shown in Figure 4A

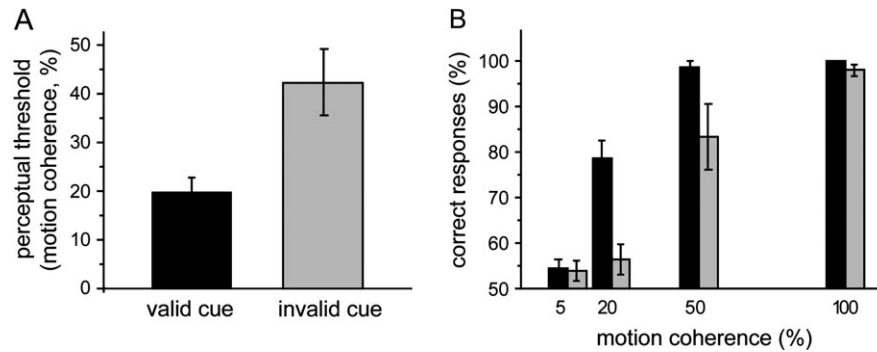


Figure 2. Behavioral results. (A) The perceptual thresholds (group means \pm SEM) for valid and invalid cueing. (B) The proportion of correct judgments for direction of motion plotted for those coherence levels for which MEG responses were collected (group means \pm SEM).

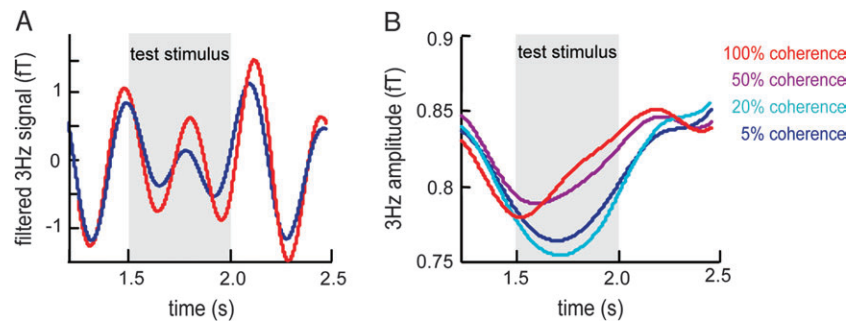


Figure 3. (A) Time course of the Gaussian filtered (3 ± 2 Hz) MEG responses averaged over all sensors of 1 hemisphere in 1 exemplary subject (red: 100% coherence, blue: 5% coherence). The difference between curves depicts the dependency of the oscillation on motion coherence with larger amplitudes for higher coherence levels. (B) Group data: Time course of the oscillation after amplitude demodulation (average over all sensors and subjects).

statistically significant dependencies on motion coherence were confined to sensors lying contralateral to the attended RDK but were absent for ipsilateral sensors. Note that visual motion was displayed in both visual hemifield and, therefore, the 2 cortical hemispheres were exposed to the same stimulus. The fact that these dependencies emphasized temporo-occipital sensors under both conditions was consistent with our earlier study (Händel et al. 2007).

In order to capture the modulation of the oscillation during the relevant time period (250–500 ms after test stimulus onset) in more detail, spectral amplitudes were extracted from those sensors that exhibited a significant influence of motion coherence under either of the 2 directions of spatial orienting. As can be drawn from Figure 4B the main effect of spatial orienting was an increase in coherence modulation of spectral amplitudes. An overall difference, however, between amplitudes derived from sensors lying ipsilateral to the attended hemifield as compared with amplitudes of contralateral sensors was not present. This effect was confirmed by a 3-way repeated-measures ANOVA with the factors motion coherence, sensor location [left or right] and sensor location relative to the attended hemifield [ipsilateral or contralateral]. Motion coherence showed a significant main effect on the measured activity ($P < 0.001$) whereas the sensor location relative to the attended hemifield did not ($P = 0.37$). Coherence modulation, however, was depending on the sensor location relative to the attended hemifield as indicated by a significant interaction of the 2 factors ($P < 0.001$). Additionally, the 3-way ANOVA showed that on average amplitudes picked up from the right cortical hemisphere were significantly higher as compared

with left hemisphere responses ($P < 0.01$), however, the interaction with neither motion coherence ($P = 0.9$) nor sensor location relative to the attended hemifield ($P = 0.36$) was significant. Post hoc analyses (paired *t*-tests) of the amplitudes presented in Figure 4B revealed significant differences for all coherence levels except the 50% stimulus with attention resulting in higher amplitudes for stimuli with high global net motion (100% coherence: $P < 0.001$) and lower amplitudes for stimuli dominated by noise (5% coherence: $P = 0.002$; 20% coherence: $P = 0.0048$).

In order to localize the sources of the 3-Hz oscillation observed during motion presentation, a beamforming method was used which compared source power of the fixation period prior to the arrow onset (0–0.5 s) with that observed in the time period of coherent motion presentation (1.5–2.0 sec). Figure 5 provides the source distributions obtained from 3 representative subjects. As can be seen, activity evoked by coherent motion was distributed and included, both, temporo-occipital and parieto-occipital areas. Activations emphasized the dorso-medial aspects of parieto-occipital cortex. More specifically, in most subjects including the examples presented in Figure 5 voxels with peak activations were clustered inferior to the parieto-occipital and in close vicinity to the transverse occipital sulcus suggesting area V3a as a main source contributing to the 3-Hz activity (Goebel et al. 1998; Braddick et al. 2000).

Discussion

Cortical oscillations like the 3-Hz signal tracked here using MEG are thought to reflect synaptic potentials and other slow

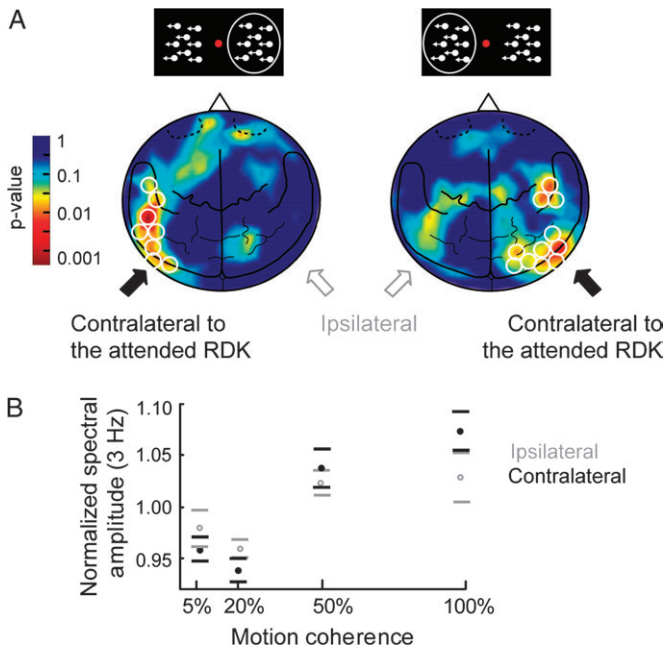


Figure 4. (A) Statistical probability mapping of spectral amplitude dependencies on motion coherence projected onto 2-dimensional MEG sensor maps (seen from above, nose up). *P* values denoting the level of statistical significance of the effect of motion coherence on spectral amplitude present during the 2nd half of test stimulus presentation (250–500 ms after test stimulus onset). *P* values were calculated from an ANOVA (see Methods) and are color-coded here in order to provide a quasi-field distribution. Distributions of *P* values are shown for the 2 directions of spatial orienting indicated by the white ellipses surrounding 1 of the RDKs in the sketches of stimuli. Note that the motion coherence of the visual stimulus was always the same covering corresponding parts of both visual hemifields and that only the attentional instruction and possibly motion direction was different. The white circles mark those sensors which revealed a significant dependency on motion coherence (2 adjacent sensors with $P < 0.05$). (B) Normalized spectral amplitudes obtained from the significant sensors marked in A (means and SEM of both the left and right marked sensors) as a function of motion coherence shown separately for sensors lying contralateral (black) and ipsilateral (gray) to the attended RDK. Because sensors over the left and right hemisphere (independent of the attentional state) showed no significant difference in coherence modulation (3-way ANOVA), responses from sensors over both hemispheres were pooled and stratified according to sensor location relative to the attended hemifield (either ipsi- or contralateral). Normalization was performed on single subject and sensor basis. Amplitudes were averaged across the 2 directions of spatial orientation and all coherence levels and then divided by the overall mean.

electric signals such as spike afterpotentials and voltage-dependent membrane oscillations largely determined by functional states of cortex and thalamus. As a rule, slower frequencies are thought to involve spatially more extensive synchronous activation of a large neuronal pool (Buszák 2006). We therefore set out to take this oscillation as a compound measure of population activity of human cerebral cortex and asked whether this measure would show signal-to-noise features correlating with the perceptual changes induced by selective attention. This attempt was motivated by the fact that the spectral amplitudes of this oscillation had shown a robust, monotonic dependency on motion coherence in a previous study (Händel et al. 2007).

A clear dependency on motion coherence was replicated in the present study, although the relationship was nonmonotonic due to the small increase of spectral amplitudes at 5% compared with 20% motion coherence, the former level not tested previously. Similar increases at low coherence levels have been reported by Rees et al. (2000) using functional

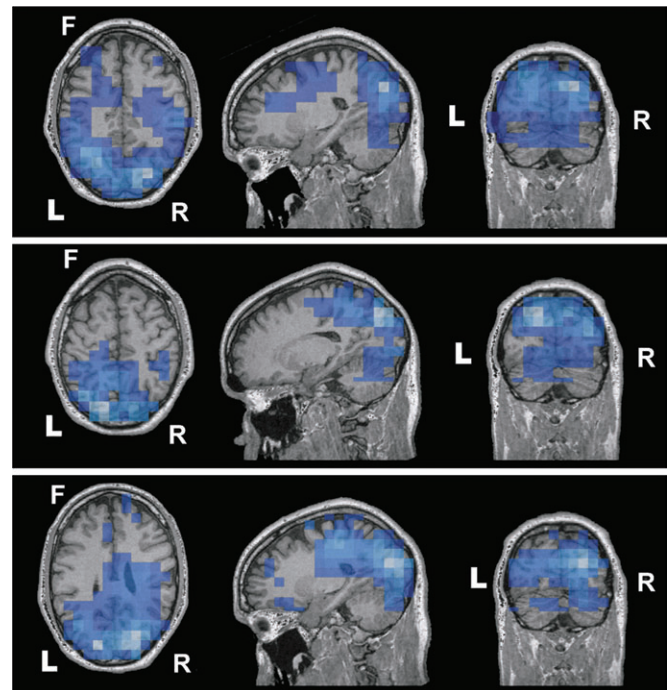


Figure 5. Spatial distribution of the motion induced 3 (± 2) Hz oscillation as revealed by minimum variance beamformer algorithms (SAM). Localization of voxels with *t* values > 2 obtained from pseudo-*t* statistics estimating the difference in source power between fixation (0–0.5 s) and coherent motion (1.5–2 s) presentation. The 3 rows show the results for 3 representative subjects plotted onto an orthogonalized and normalized anatomic magnetic resonance image of 1 of the subjects (R: right; L: left; F: frontal). The brighter the blue-colored voxels, the more significant the difference in source power for motion presentation compared with fixation. The 3 different sectional planes in the given subject are attached to the voxel with the highest *t* value.

magnetic resonance imaging. The authors reported a linear relationship between BOLD responses and motion coherence in areas MT+, V2, and other visual areas but found 2nd-order correlations in the middle occipital gyrus and area V3a. In fact, it is tempting to speculate that the emphasis on dorsomedial parieto-occipital cortex such as observed for the 3 subjects presented in Fig. 5 might reflect dominating responses of area V3a giving rise to a higher order correlation. In any case, the relationship observed here is likely to reflect a weighted average of contributions from different cortical areas. This interpretation is fully in line with the widespread activation (see again Fig. 5) which emphasized not only parieto-occipital but also temporo-occipital cortex and which was in good agreement with the distributed motion induced activation patterns obtained from other studies using functional magnetic resonance imaging (fMRI) (e.g., Sunaert et al. 1999, Braddick et al. 2000, Rees et al. 2000).

The nonlinearity of the dependency notwithstanding, we may ask whether the oscillation changed in a way corresponding to the perceptual differences induced by selective attention. Specifically, if the 3-Hz oscillation were indeed a reflection of compound activity giving rise to the altered discrimination performance its amplitude should meet the following predictions: 1st, as argued in the Introduction, an improvement in motion perception should be indicated by an increase of coherence dependency. Second, amplitudes for a given coherence level should be higher with attention provided that

the perceptual performance would be improved relative to the same level when unattended. Third, along the line of arguments put forward by Cook and Maunsell (2002), behavioral performance should follow changes in neuronal responses, whether those arise from stimulus differences or changes in behavioral state. In other words, the neuronal responses should be more or less constant for conditions that were the same in behavioral terms, even if the stimulus features were different.

Our results are clearly in accordance with the 1st prediction: The main effect of misdirected selective attention was a striking loss of coherence dependency, importantly, without any attention induced change in the overall activity such as has been reported for instance by previous fMRI studies (Tootell et al. 1998; Smith et al. 2000). However, the other 2 predictions are violated. Quite contrary to the 2nd, the amplitudes obtained for the coherence level with the strongest perceptual differences (the 20% motion coherence level, see Fig. 2*B*) were smaller with attention as compared with misdirected attention (Fig. 4*B*). Likewise, amplitudes for similar behavioral performances were by no means constant as exemplified by the responses obtained at 20% and 50% motion coherence. The behavioral performance at the 20% level with attention was virtually the same as the 1 possible without attention at the 50% level (Fig. 2*B*). The spectral amplitudes of this pair of conditions, however, were quite different (Fig. 4*B*). The interpretation that the modulation of the neuromagnetic response induced by attention reflects the change in percept, therefore, seems only partially supported at 1st glance.

In order to come up with an explanation to this seemingly conflicting pattern of results we have to consult both human and animal studies that have previously been addressing the influence of selective attention on motion perception. Unfortunately, a comparison of the present results with former human studies is possible only to a limited extent. On the one hand, it has been shown that motion coherence can induce differential activity in various visual areas (fMRI: Rees et al. 2000; Braddick et al. 2001; EEG and MEG: Niedeggen and Wist 1999; Patzwahl and Zanker 2000; MEG: Maruyama et al. 2002; Nakamura et al. 2003; Aspell et al. 2005) and on the other hand, studies on attention have shown that visually evoked potentials (e.g., Neville and Lawson 1987; Anllo-Vento and Hillyard 1996; Torriente et al. 1999) as well as BOLD signals (e.g., Corbetta et al. 1990; Rees et al. 1997) induced by motion stimuli are modulated by attention. However, as far as we can tell the effects of attention on brain activity depending on the signal-to-noise characteristics of visual motion have not been investigated so far in humans.

The most direct comparison in this respect is offered by a monkey study by Cook and Maunsell (2002). In their carefully performed single-cell recording study the authors demonstrated response enhancement not only for coherent motion but even for motion stimuli lacking any coherence. This result seems to be in conflict with our differential effect of selective attention depending on motion coherence. It is important to note, however, that the MEG signal analyzed here represents a compound measure of responses to both coherent and incoherent motion with the latter comprising visual motion in all possible directions. In fact, a major difference between this human study and previous monkey experiments is that only in the animal it is possible to adjust the stimuli to the preferences of the neuron under study. However, by matching stimuli to the preferred directions of the neuron (Cook and Maunsell

2002) the influence of selective attention on motion coherence has only been examined for a particular selection of cells. On the other hand, the coherence modulation of neurons with deviant preferences has not been tested but might nevertheless contribute to the attentional effect (Martinez-Trujillo and Treue 2004). We suggest that the change in coherence dependency observed here is a reflection of all the neurons exhibiting any motion preference and that the responses to coherent and incoherent motion, respectively, might be differentially modulated by selective attention. Accordingly, the increase in spectral amplitude observed here at 100% motion coherence would reflect response (signal) enhancement such as reported by many studies (e.g., Treue and Maunsell 1996; Tootell et al. 1998; Smith et al. 2000; Cook and Maunsell 2002). On the other hand, the decrease at low coherence levels (20%, 5%) would indicate noise reduction outweighing enhancement of the response to a weak coherence signal. For this interpretation to be valid, knowledge on how to disentangle signal (coherent motion) from noise (incoherent motion) must be available. Indeed, in our paradigm such knowledge was offered by the fact that coherent motion always occurred in horizontal direction. Importantly, attention based on motion direction has been demonstrated in single-cell recordings to differentially modify neural response rates: those neurons with a preference close to the attended feature are going to experience an enhanced response gain but others for which the attended feature is different from the neuron's preference will be reduced in their firing rate (Martinez-Trujillo and Treue 2004; Treue and Martinez-Trujillo 2006). In this way, the present observation of a differential change in neural response depending on motion coherence is fully in line with the concept of a push-pull effect across the population as suggested from single-cell recordings.

We should emphasize that interpretations other than the 1 developed above are also conceivable. An alternative possibility, for example, could be that selective attention affects the different cell types present in visual cortex such as "global motion" and "local motion" neurons (Born and Tootell 1992) in different, potentially opposing ways. Given the fact that visual receptive fields can be dynamically modified by spatial attention (Womelsdorf et al. 2006) and given that population responses (such as MEG measures) critically depend on the relationship between stimulus size and receptive field properties (and their surrounds) different scenarios fully accounting for the present findings could be envisaged. Another question worthwhile studying in future experiments is whether or not the same attentional mechanisms suggested here for coherent motion perception also apply to other types of perceptual processes such as the global processing of nonmoving visual stimuli ("form coherence," Braddick et al. 2001).

Conclusions

In summary, we tested the effects of selective attention on MEG responses in man picked up from extrastriate cortex and correlating with motion coherence. The paradigm applied carefully controlled for parameters unrelated to selective attention such as alertness or eye movements. The modulation of motion perception induced by selective attention was paralleled by changes in coherence dependency of the MEG response. Specifically, attention directed to a given hemifield increased and decreased the coherence modulation of the MEG

response over contralateral and ipsilateral visual cortex, respectively, indicating a change in the neuronal signal-to-noise ratio at the population level.

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Notes

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Address correspondence to Dr Thomas Haarmeier, Department of Cognitive Neurology, Hertie Institute for Clinical Brain Research, Klinikum Schnarrenberg, Hoppe-Seyler-Straße 3, 72076 Tübingen, Germany. Email: thomas.haarmeier@uni-tuebingen.de.

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