Perception of Self-Motion From Peripheral Optokinetic Stimulation Suppresses Visual Evoked Responses to Central Stimuli

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Thilo, Kai V., Andreas Kleinschmidt, and Michael A. Gresty. Perception of self-motion from peripheral optokinetic stimulation suppresses visual evoked responses to central stimuli. J Neurophysiol 90: 723–730, 2003; 10.1152/jn.00880.2002. In a previous functional neuroimaging study we found that early visual areas deactivated when a rotating optical flow stimulus elicited the illusion of self-motion (vection) compared with when it was perceived as a moving object. Here, we investigated whether electrical cortical responses to an independent central visual probe stimulus change as a function of whether optical flow stimulation in the periphery induces the illusion of self-motion or not. Visual-evoked potentials (VEPs) were obtained in response to pattern-reversals in the central visual field in the presence of a constant peripheral large-field optokinetic stimulus that rotated around the naso-occipital axis and induced intermittent sensations ofvection. As control, VEPs were also recorded during a stationary peripheral stimulus and showed no difference than those obtained during optokinetic stimulation. The VEPs during constant peripheral stimulation were then divided into two groups according to the time spans where the subjects reported object- or self-motion, respectively. The N70 VEP component showed a significant amplitude reduction when, due to the peripheral stimulus, subjects experienced self-motion compared to when the peripheral stimulus was perceived as object-motion. This finding supplements and corroborates our recent evidence from functional neuroimaging that early visual cortex deactivates when a visual flow stimulus elicits the illusion of self-motion compared with when the same sensory input is interpreted as object-motion. This dampened responsiveness might reflect a redistribution of sensorial and attentional resources when the monitoring of self-motion relies on a sustained and veridical processing of optic flow and may be compromised by other sources of visual input.

INTRODUCTION

Multiple sensory systems subserve the perceptual reconstruction of self-motion. Vestibular, somatosensory, and visual modalities all provide input that can be relevant for the computation of self-motion and this multisensory synthesis is reflected in intimate interactions at the neural level (de Waele et al. 2001; Dichgans and Brandt 1978). In particular, the visual and the vestibular sensory systems share various processing stages in the CNS. Yet, the visual sense alone can underlie self-motion perception when this self-motion is of a type where the input provided by other spatial senses, such as the vestibular and proprioceptive systems, is not informative. Accordingly, uniform and sustained motion of the visual environment, resembling optic flow patterns produced by locomotion, is a powerful stimulus to induce the illusory perception of contralateral self-motion, or vection (Dichgans and Brandt 1978). This can frequently be experienced in motion simulators and when seated in a stationary railway carriage where the sight of a moving train elicits the perception of self-motion. During sustained optokinetic stimulation around the sagittal, or x-axis, the perception of circularvection does not typically continue uninterruptedly but is spontaneously interspersed by periods of perceived object-motion and concurrent self-stationarity (Cheung and Howard 1991; Finke and Held 1978; Thilo et al. 1999).

A number of electrophysiological studies investigating vestibular function and visual-vestibular interaction by means of evoked potentials have been conducted in the past using optokinetic stimulation (Hood 1983; Mergner et al. 1989), vestibular stimulation on earth (Hood 1983; Hood and Kayan 1985; Mergner et al. 1989; Probst and Wist 1990; Probst et al. 1995, 1997), and during microgravity induced by parabolic flight (Probst et al. 1996). These have identified characteristic scalp responses to optokinetic and rotational vestibular stimulation as well as a modulation of evoked potential parameters by head orientation relative to the gravito-inertial vector. More recently, the neural responses to rotatory optokinetic stimulation (Brandt et al. 1998) and the correlates of visually induced self-motion perception (Kleinschmidt et al. 2002) have been investigated using functional neuroimaging. In this latter study, constant optokinetic stimulation around the sagittal axis intermittently elicited the perception of self-rotation, and we contrasted activity levels between the perception of object-motion and that of self-motion during identical sensory input. We found a deactivation in parieto-insular vestibular cortex (PVC; Bottini et al. 2001; Fasold et al. 2002; Grüsser et al. 1990; Gulddin and Grüsser 1998) but also in striate and early extrastriate cortex during the perception of self-motion as compared with perceived object-motion. In the anterior part of lateral occipito-temporal cortex (human motion complex) and in dorsomedial parieto-occipital cortex (putative V6/PO), however, activity
levels during vection remained unchanged compared with the perception of the same sensory input as motion in the environment.

In the present study we used a VEP paradigm to further characterize the functional behavior of early occipital cortex during the two contrasting perceptual states induced by optokinetic stimulation. In comparison to the electrophysiological and neuroimaging studies mentioned above, the novelty of this approach was that we studied the influence of the percept evoked by large-field peripheral sensory input on the processing of a central stimulus. In other words, we tested whether the response to continuous pattern-reversal in the central visual field would be affected by the perceptual bistability of simultaneous and sustained optokinetic stimulation in the frontal plane, subtending a large portion of the peripheral visual field (Fig. 1A). This peripheral sensory input is perceptually ambiguous and results in spontaneous alternations between the subjective percepts of object-motion or self-motion. The electrophysiological responses to the probe stimulus in the central visual field were grouped according to whether they were obtained during the perceived periods of object-motion or those of self-motion. Based on our earlier findings, we hypothesized that during vection responses to the visual stimulus should be attenuated. Thus this study investigated whether the bistable perceptual interpretation of a moving visual environment forms a context-dependent influence on early cortical processing of simultaneously present, but unrelated, visual input.

METHODS

Subjects

Five women and three men, from 24 to 29 yr of age (mean 26.0 yr), without any history of relevant neurological or sensory disease, participated in the experiment. All had normal or corrected-to-normal vision. Informed consent had been obtained from all subjects prior to the start of the experiment.

Apparatus

The optokinetic stimulus consisted of an alternating pattern of black and white radial sectors, spaced at equal intervals, that was back-
projected onto a screen subtending 110° of visual angle horizontally and 110° vertically, refreshing at a rate of 60 Hz. The stimulus rotated around an earth-horizontal axis that was aligned with the subjects’ line of sight. The white and black stimulus elements had luminances of 0.11 and 0.08 cd/m², respectively. The checkboard-reversal stimulus was presented on an LCD monitor, 287 mm wide and 215 mm high, that was positioned approximately 2 cm in front of the optokinetic stimulus and centered with respect to the subjects’ line of sight. The checkboard pattern consisted of 32 vertical columns and 24 horizontal rows of alternating black and white squares that inverted continuously every 750 ms and subtended approximately 45° of visual angle. At its center was a medium gray circular fixation target with a diameter a quarter of the side length of a square. Figure 1A gives a schematic overview of the experimental setup.

Electrophysiological recording

Following skin preparation, 8 mm silver/silver chloride electrodes were fixed to the scalp according to the 10–20 system (Jasper 1958) at positions O₁ (occipital left), O₂ (occipital midline), O₃ (occipital right), and F₉ (frontal midline) using adhesive conductive electrode paste. Additional electrodes were attached to each earlobe and connected together as inactive reference. Impedances between pairs of electrodes were below 5 kΩ. Differential recordings were obtained between the electrode pairs O₁-F₉, O₁-F₉, O₂-F₉, and F₉-earlobes at a gain of 50 μV/V, a high-cut frequency of 30 kHz, and a time constant of 500 ms. As a control of peripheral optokinetic stimulation as originating from environment or self-motion, horizontal and right monocular vertical DC-electrooculogram was monitored continuously every 750 ms and subtended approximately 45° of visual angle.

Procedure

Subjects were seated at a distance of 68 cm from the fixation target, and thus approximately 70 cm from the background optokinetic display, with their heads supported by a chin rest. They were instructed to look at the fixation target and to avoid eye blinks and other sources of artifacts. Sessions began with the recording of 200 pattern-reversal sweeps while the optokinetic stimulus was stationary. After a break, 600 sweeps were recorded with the optokinetic stimulus revolving clockwise at a velocity of 45°/s. For the duration of this trial, subjects signaled the perception of object-motion versus that of circularvection by switching a hand-held dial between two predefined settings. See Fig. 1B for an example of the time-course of an experimental session.

Bistable percepts of ambiguous visual stimuli are not always mutually exclusive and sometimes both perceptual interpretations can coexist simultaneously, especially during transition periods (Blake and Logothetis 2001). During optokinetic stimulation, the perception of self-motion often develops gradually with a simultaneously perceived slowing of environment- or object-motion (Wertheim 1994). Despite this gradual build-up, subjects were required to decide in a binary, or all-or-nothing, manner whether they perceived the optokinetic stimulation as originating from environment or self-motion according to the perceived prevalent dominance. This was done to ensure a simple and intuitive task as well as to permit statistical analysis of the reported perceptual states as a categorical variable, consistent with our recent work on bistable percepts across sensory modalities (e.g., Thilo and Gresty 2002) as well as with studies on purely visual ambiguities and binocular rivalry (e.g., Leopold et al. 2002).

Data analysis

All recordings were analyzed and processed off-line after data acquisition had terminated. Sweeps containing artifacts, mainly caused by eye blinks, were excluded following visual inspection of the raw data. Subsequently, the five sweeps preceding as well as following each transition between perceptual states were excluded to avoid contamination of the signal by components related to transitional states and their reporting, which involved a motor response. Following this, condition-specific evoked potentials were computed by averaging trials for two subsequent levels of analysis. At the first level of analysis, we addressed whether the presence of constant peripheral sensory input per se affected the VEP in response to central pattern reversal. Accordingly, we averaged the sweeps that were recorded while the optokinetic stimulus was stationary (VEP-STAT) and the sweeps sampled during optokinetic stimulation (VEP-OKS), irrespective of the perceptual state reported by the subjects. At the second (embedded) level of analysis, we addressed whether the perceptual state that this peripheral sensory input resulted in would affect the VEP. Accordingly, the entirety of sweeps recorded during optokinetic stimulation was split into two separate groups as a function of the concurrent perceptual states experienced by the subjects. We then averaged the sweeps that were recorded while subjects reported the perception of object-motion (VEP-OM) and compared them to the average of the sweeps during which circularvection was perceived (VEP-SM). In other words, VEP-OKS was split up into VEP-OM and VEP-SM.

Following three-point smoothing, baseline was calculated as the average signal obtained during the 50 ms preceding pattern reversal. The first negative inflection (N70) and the first positive (P100) inflection of the signals were determined automatically. Latencies relative to pattern-reversal and amplitudes relative to baseline were computed for each subject and conditioned as defined above.

RESULTS

Psychophysical data

Following optokinetic stimulation onset, all subjects reported perceiving rollvection with an average onset latency of 11.0 s (SE, 4.8 s). During the 450 s of optokinetic stimulation, subjects perceived circularvection for, on average, 215.6 s (SE, 16.3 s).

Evoked potentials

After rejections of sweeps containing artifacts and of those that were acquired close to perceptual transitions, the individual averages obtained were computed from 152 to 355 single sweeps. A detailed list containing mean onset latencies of the VEP N70 and P100 components during moving versus stationary peripheral optokinetic stimulation and during the perception of object-motion versus circularvection for the different electrode positions is presented in Table 1. The corresponding baseline-to-peak amplitudes are listed in Table 2. It should also be noted that in the two-way repeated measures analyses of variance (ANOVA) presented subsequently no interaction reached significance unless stated otherwise. See Fig. 2 for a sample series of evoked potentials obtained in a single subject at different electrode positions, stimulation conditions, and perceptual dominances.

Peripheral visual field stationarity versus optokinetic stimulation—N70

AMPLITUDE. The baseline-to-peak amplitudes of the first negative inflection of the VEP were not significantly affected by rotation of the optokinetic stimulus as demonstrated by a two-way repeated measures ANOVA. Averaged across occipital electrode positions, mean amplitudes were −3.8 μV during
stationarity and $-3.4 \mu V$ at a rotating background ($F_{1,7} < 1$). A significant main effect of electrode position ($O_1$: $-3.2 \mu V$; $O_2$: $-5.2 \mu V$; $O_Z$: $-2.3 \mu V$; $F_{2,14} = 5.7; P < 0.05$) was found and demonstrated ex post to be due to a significant quadratic contrast ($F_{1,7} = 7.1; P < 0.05$). Figure 3 depicts the average amplitudes of the VEP N70 component across all subjects and electrode positions.

**PEAK LATENCY**. A similar, nonsignificant, result was obtained for the corresponding peak latencies with values of 62.0 ms during stationary trials and 61.8 ms during optokinetic stimulation averaged across electrode positions ($F_{1,7} < 1$, 2-way repeated measures ANOVA). There was a significant main effect of electrode position ($F_{2,14} = 4.1; P < 0.05$) on onset latency with a latency of 58.4 ms at $O_1$, 67.1 ms at $O_Z$, and 60.2 ms at $O_2$. This main effect is explained by the increased latency at the midline electrode position as demonstrated by a significant post-hoc quadratic contrast ($F_{1,7} = 10.3; P < 0.05$).

**Peripheral visual field stationarity versus optokinetic stimulation—P100**

**AMPLITUDE**. Motion of the visual surround had no significant effect on baseline-to-peak amplitudes which were, on average, 11.6 $\mu V$ without and 11.0 $\mu V$ with optokinetic stimulation ($F_{1,7} = <1$). There was, however, a significant effect of electrode position on P100 amplitudes, which were 9.6 $\mu V$ at $O_1$, 12.4 $\mu V$ at $O_Z$, and 12.0 $\mu V$ at $O_2$ ($F_{2,14} = 6.3; P < 0.05$).

**PEAK LATENCY**. Mean peak onset latencies for the first positive inflection were, averaged across sites, 97.2 ms without and 95.8 ms with optokinetic stimulation ($F_{1,7} = 1.1$; n.s.). Electrode position also had no significant effect on onset latencies ($O_1$: 96.8 ms; $O_2$: 95.3 ms; $O_Z$: 97.3 ms; $F_{2,14} = 1.6$; n.s.).

**Perception of object-motion versus circularvection—N70**

**AMPLITUDE**. During perception of object-motion, baseline-to-peak amplitude of the N70 component was $-3.8 \mu V$, whereas during circularvection the inflection was $-3.0 \mu V$ and therefore significantly lower as demonstrated by ANOVA ($F_{1,7} = 7.6; P < 0.05$). A main effect of recording site also was significant ($F_{2,14} = 5.0; P < 0.05$) with corresponding values being $-3.0 \mu V (O_1)$, $-5.0 \mu V (O_2)$, and $-2.3 \mu V (O_Z)$. Figure 3 shows the group means of the N70 amplitudes across perceptual states and electrode sites.

**PEAK LATENCY**. The perceptual state subjects experienced while their brain activity was recorded had a significant effect on the N70 peak latency. During reported object-motion, mean latency was 63.3 ms and during circularvection it was marginally reduced to 62.8 ms ($F_{1,7} = 6.0; P < 0.05$). Although statistically significant, there are no conceivable functionally relevant implications of an average latency difference of 0.5 ms across subjects, especially when considering that signals were recorded at a sample rate of 1 kHz. Averaged over perceptual states, mean latencies obtained at the different electrode positions were 63.1 ms at $O_1$, 65.9 ms at $O_Z$, and 60.0 ms at $O_2$. There was also a significant main effect of recording site ($F_{2,14} = 3.84; P < 0.05$) with a significant quadratic post-hoc contrast ($F_{1,7} = 12.1; P < 0.05$).

**Perception of object-motion versus circularvection—P100**

**AMPLITUDE**. During perception of object-motion, average P100 amplitude was 11.0 and 11.2 $\mu V$ duringvection with no

### Table 1.

Means and standard errors (in parentheses) of the onset latencies (ms) of the N70 and P100 components of the checkerboard reversal visual-evoked potential during the perception of object-motion (OM) versus self-motion (SM) and during a stationary peripheral visual field (ST) versus rotating optokinetic stimulation (OKS).

<table>
<thead>
<tr>
<th>Electrode Position</th>
<th>OM</th>
<th>SM</th>
<th>OM</th>
<th>SM</th>
<th>OM</th>
<th>SM</th>
<th>OM</th>
<th>SM</th>
</tr>
</thead>
<tbody>
<tr>
<td>N70</td>
<td>63 (2)</td>
<td>59 (4)</td>
<td>66 (3)</td>
<td>66 (3)</td>
<td>62 (3)</td>
<td>59 (4)</td>
<td>59 (6)</td>
<td>60 (5)</td>
</tr>
<tr>
<td>P100</td>
<td>96 (2)</td>
<td>96 (3)</td>
<td>95 (2)</td>
<td>95 (2)</td>
<td>96 (2)</td>
<td>96 (2)</td>
<td>95 (3)</td>
<td>93 (6)</td>
</tr>
<tr>
<td>Peripheral Field</td>
<td>ST OKS</td>
<td>ST OKS</td>
<td>ST OKS</td>
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<tr>
<td>N70</td>
<td>57 (4)</td>
<td>63 (2)</td>
<td>68 (2)</td>
<td>66 (2)</td>
<td>61 (3)</td>
<td>59 (4)</td>
<td>51 (5)</td>
<td>55 (6)</td>
</tr>
<tr>
<td>P100</td>
<td>98 (3)</td>
<td>96 (2)</td>
<td>95 (2)</td>
<td>95 (2)</td>
<td>98 (3)</td>
<td>96 (2)</td>
<td>96 (2)</td>
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### Table 2.

Means and standard errors (in brackets) of the baseline-to-peak amplitudes ($\mu V$) of the N70 and P100 components of the checkerboard reversal VEP during the perception of object-motion (OM) versus self-motion (SM) and during a stationary peripheral visual field (ST) versus rotating optokinetic stimulation (OKS).

<table>
<thead>
<tr>
<th>Electrode Position</th>
<th>OM</th>
<th>SM</th>
<th>OM</th>
<th>SM</th>
<th>OM</th>
<th>SM</th>
<th>OM</th>
<th>SM</th>
</tr>
</thead>
<tbody>
<tr>
<td>N70</td>
<td>3.4 (1.0)</td>
<td>2.5 (1.0)</td>
<td>5.3 (1.3)</td>
<td>4.6 (1.2)</td>
<td>2.6 (0.8)</td>
<td>2.0 (0.8)</td>
<td>−1.6 (0.5)</td>
<td>−1.2 (0.6)</td>
</tr>
<tr>
<td>P100</td>
<td>9.1 (1.3)</td>
<td>9.5 (1.3)</td>
<td>12.2 (1.7)</td>
<td>12.4 (1.8)</td>
<td>11.7 (1.4)</td>
<td>11.7 (1.5)</td>
<td>−3.3 (0.7)</td>
<td>−3.4 (0.8)</td>
</tr>
<tr>
<td>Peripheral Field</td>
<td>ST OKS</td>
<td>ST OKS</td>
<td>ST OKS</td>
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<td>ST OKS</td>
<td>ST OKS</td>
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</tr>
<tr>
<td>N70</td>
<td>3.4 (1.1)</td>
<td>3.0 (0.9)</td>
<td>5.4 (1.5)</td>
<td>4.9 (1.3)</td>
<td>2.4 (0.9)</td>
<td>2.2 (0.8)</td>
<td>−1.1 (0.5)</td>
<td>−1.3 (0.5)</td>
</tr>
<tr>
<td>P100</td>
<td>9.9 (1.5)</td>
<td>9.2 (1.3)</td>
<td>12.6 (1.8)</td>
<td>12.2 (1.7)</td>
<td>12.3 (1.7)</td>
<td>11.7 (1.4)</td>
<td>−4.2 (0.8)</td>
<td>−3.2 (0.7)</td>
</tr>
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</table>
main effect of perceptual state detected by ANOVA ($F_{1,7} < 1$). Electrode position had a highly significant effect with amplitudes being 9.3 $\mu$V at $O_1$, 12.3 $\mu$V at $O_2$, and 11.7 $\mu$V at $O_2$ ($F_{2,14} = 7.2; P < 0.01$).

**Peak Latency.** No effect of perceptual state (OM: 95.7 ms; SM: 95.4 ms; $F_{1,7} < 1$) nor of electrode position ($O_1$: 95.5 ms; $O_2$: 95.1 ms; $O_3$: 96.0 ms; $F_{2,14} < 1$) on peak latency of the first positive inflection was detected.

**FIG. 2.** Sample of visual evoked potentials in a single subject at the different comparisons performed. Note the difference in amplitude of the first negative (upward) inflection between the traces obtained during perception of object-motion and circularvection (top traces). Also note the absence of a difference when comparing the potentials recorded during a stationary visual surround with optokinetic stimulation (bottom traces).

**FIG. 3.** Means and standard errors of the amplitudes of the N70 components of the VEP during stationary vs. rotating optokinetic stimulation and during the perception of object-motion versus circularvection.
**Contribution of the prefrontal electrode site**

Since all results described so far were obtained as differential recording between an occipital electrode site (O2, O1, O3) and another electrode placed medially over the prefrontal cortex (Fp2), any potential recorded is reflecting an electrical dipole between occipital and frontal regions. To determine to what extent the results observed were caused by changes in electrical activity underlying the prefrontal electrode, amplitudes and latencies of the N70 and P100 peaks were analyzed for the differential recording between the prefrontal electrode position and the linked earlobe electrodes, serving as inactive reference. Therefore paired t-tests, comparing stationarity versus optokinetic stimulation and perception of object-motion versus circularvection, were computed for the latencies and amplitudes of the N70 and P100 components separately. No comparison demonstrated a significant effect of optokinetic stimulation or perceptual state on the frontal electrode site (all P > 0.05).

**DISCUSSION**

The main finding of this experiment is that, during constant peripheral optokinetic stimulation, the amplitude of the first negative inflection of the visual-evoked response to central stimulation was significantly reduced during vection compared with the perception of object-motion. Optokinetic stimulation in itself, however, did not influence any parameter of the N70 component. The P100 component was not affected by presence or absence of optokinetic stimulation in the periphery, nor by the percept of self- versus object-motion elicited by large-field optokinetic stimulation. In addition, a general tendency was observed for N70 latency to be increased, and for its amplitude to be raised, at the midline electrode position. P100 latency, on the contrary, was not influenced by electrode position but its amplitude, too, was elevated at electrode position O2.

The neuronal generators of the N70 and P100 components of the pattern-reversal VEP are likely to be located in primary visual cortex (Brodmann area 17). In patients with lesions restricted to striate cortex, these components are generally absent or abnormal (Aldrich et al. 1987), whereas in patients with lesions in visual association cortex they are preserved (Bodis-Wollner et al. 1977). The two components seem functionally dissociated since patients with a preserved N70 and an abnormal P100 have been reported (Celesia et al. 1980, 1982). Intracortical recordings in monkeys have demonstrated that the N70 component reflects excitatory postsynaptic potentials of stellate cells in primary visual cortex layer 4C (Schroeder et al. 1991). These cells receive input from primary thalamic afferents, from other striate cortical layers, and from extrastriate cortex. The ensuing P100 component presumably reflects inhibitory postsynaptic potentials of pyramidal neurons in layers 2 and 3 (Schroeder et al. 1991), possibly mediated by GABAergic transmission (Halgren 1990; Zemon et al. 1986). At this level of specification it is not possible to distinguish the relative contributions of the magnocellular and parvocellular pathways to the N70 component since geniculothalamic fibers of both systems terminate in striate cortex layer 4C—the magnocellular pathway in layer 4Cα and the parvocellular pathway in layer 4Cβ (Lamme et al. 1998).

From a physiological perspective, the finding of reduced net excitation in primary visual cortex during the perception of circularvection fits well with the observation of a deactivation in calcarine cortex during vection as demonstrated in our previous experiment using fMRI. It has recently been established that the BOLD fMRI response of monkey visual cortex is best accounted for by transient local field potentials, which suggests that the fMRI signal is a probable marker of input to, and intrinsic synaptic activity in, a given neuronal population (Logothetis et al. 2001).

It has been well established that parieto-insular vestibular cortex undergoes deactivation during visually induced self-motion sensation (Brandt et al. 1998; Kleinschmidt et al. 2002). The functional interpretation of this reduction of vestibular cortical sensitivity has been that it could protect against irrelevant and presumably detrimental vestibular input from involuntary head accelerations and thereby improve computation of self-motion from vision alone (Brandt et al. 1998; Dieterich and Brandt 2000). Our previous results with functional neuroimaging and the results presented here suggest that this general notion of reduced susceptibility to “noise” input during self-motion might also apply to processes within the visual modality. To maintain an uncontaminated perception of self-motion, the sensorial weight might be shifted away from visual processing of distracting visual motion signals.

Another functionally important adjustment during optokinetic stimulation is the generation of eye movements. Rotation of the visual environment in the frontal plane elicits involuntary and reflexive torsional optokinetic eye movements (Brecher 1934; Morrow and Sharpe 1993). Although our introduction of a stationary reference in the central visual field would have dampened the gain and amplitude of torsional eye movements to some degree, the major drive for optokinetic torsion stems from the retinal periphery and a large proportion of nystagmus would have been preserved (Suzuki et al. 2000; Wade et al. 1991). Torsional optokinetic nystagmus is performed at a gain far too low to enable efficient slow-phase pursuit during visual field rotation and thus attenuates retinal motion stimulation only by about 10%. In previous studies, we have demonstrated that optokinetic nystagmus performs systematic changes when observers switch between perceptual states. During vection as opposed to perceived object-motion, mean eye position deviates more in an anticipatory direction (Thilo et al. 2000, 2002) and, in the case of torsional nystagmus, slow phase gain is enhanced, which necessarily also corresponds to an increase in the velocity, amplitude, or frequency of (saccadic) nystagmus fast phases (Thilo et al. 1999). Hence, our previous observations raise the question whether the changes in neural activity observed here might be not directly related to the differential perception of visual motion but be attributable to percept-dependent adjustments in oculomotor behavior and the ensuing changes in retinal image slip. The latter source of artifact, i.e., a change in retinal stimulation, can be ruled out because optokinetic stimulation was constant and would not have been reflected in VEs averaged to the reversals of the central checkerboard pattern. Furthermore, the fact that pattern reversals occurred during eye movements would, if anything, result in greater visual stimulation by virtue of added retinal slip and not be expected to reduce the sensory cortical response.

Percept-related differences in eye movements are equally unlikely to account for the neural response changes found, since although there was a significant reduction of negativity in
the evoked potential during circularvection in comparison to the perception of object-motion, no such effect was found when the response during optokinetic stimulation was compared with that obtained during a stationary peripheral visual field. Irrespective of the resulting percept, rotation of the stimulus induces torsional optokinetic nystagmus and therefore creates a fundamental change in oculomotor behavior that may exert a suppressive influence on sensory processing in visual areas (Gallant et al. 1998). In our experiment, the difference in torsional nystagmus was much greater when comparing the responses during optokinetic versus stationary background (nystagmus present vs. absent) than when comparing those during the two different perceptions of optokinetic stimulation in the background (nystagmus gain increase of 20–40% during vection). Therefore the subtle changes of torsional nystagmus that accompany the alternations between object- and self-motion cannot account for the differences in the VEPs that were recorded during these two perceptual states. In summary, these considerations underline the finding that the differential activation patterns observed here as well as using fMRI (Kleinschmidt et al. 2002) cannot be explained by the changes in torsional optokinetic nystagmus, which is facilitated during circularvection, nor by the resulting changes in retinal image slip.

The claim that the VEP changes observed in response to central stimulation are not caused by a change in retinal stimulus does not contradict the fact that the N70 component is generated by excitation of target neurons of the optic radiation. A large body of evidence illustrates the influence of feedback projections onto primary visual cortex neurons that originate in other layers of striate cortex as well as in extrastriate visual and higher order areas as parietal cortex (Lamme et al. 1998) mediating, among others, attentional phenomena (Ashbridge et al. 1997). Although likely to be involved in the evoked potential changes observed, feedback projections from higher cortical areas are not necessarily the only mechanism involved. Attentional effects have also been shown to be mediated by feedforward gating through the thalamus, presumably relayed via the thalamic reticular nucleus (TRN) (Guillery and Sherman 2002; Guillery et al. 1998). Furthermore, the lateral geniculate nucleus (LGN) of the thalamus could itself be involved in a possible modulatory influence since it not only receives input from retinal afferents but also from striate cortex and subcortical sources such as the TRN and the superior colliculus (SC). All of these would favor the LGN as a candidate early site for the action of top-down influences on visual information processing. In support of this proposition, covert spatial attention has recently been shown to modulate fMRI responses in the human LGN (O’Connor et al. 2002) and it has been hypothesized that the LGN is a likely site of saccadic suppression, the reduction of mainly magnocellular components of visual sensitivity during rapid gaze shifts (Burr et al. 1994; Ross et al. 1996, 2001). However, further specific studies would be needed to elucidate conceivable analogies between our observation and the phenomenon of saccadic suppression.

Whatever the precise routing of the effect we observed for the N70 component, our experimental result is likely to be evidence for a context-dependent modulation (self- or object-motion) of early visual cortical processing of sensory input. Such mechanisms seem to follow a general principle and are not confined to specific functional settings. For instance, Rees et al. (1997) have shown that the attentional demand, or load, of linguistic processing of visual stimuli presented in the central visual field influences the degree to which distracting irrelevant motion stimulation in the peripheral visual field translates into activity in the human motion complex (hMT+) at the occipito-temporal junction. When cognitive load by the task was high, the same visual motion input yielded less hMT+ activation than when the load was low. The roles of central and peripheral visual input were reversed in our experiment as we studied the modulation of constant central input as a function of the bistable perceptual interpretation of an equally constant peripheral input. Yet, the functional interpretation may also be related to attention in that the processing of visual information for the purpose of reconstructing our ego-motion presumably enjoys high attentional priority, thus suppressing the resources otherwise dedicated to processing of items in the visual scene.

In conclusion, the finding that early excitation in primary visual cortex is reduced during perceived self-motion (vection) provides electrophysiological evidence that is in accordance with our functional neuroimaging experiment in which occipital cortex was less activated during the perception of self-motion than during the perception of object-motion when subjects viewed constant rotary optokinetic stimulation. This may reflect a top-down redistribution of attentional resources, indicating their active recruitment by visual processing of self-motion and the concomitant suppression of processing of other sources of irrelevant visual input in the environment.

**DISCLOSURES**

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