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RESEARCH ARTICLE

Michael B. Hoffmann · Michael Bach

The distinction between eye and object motion is reflected by the motion-onset visual evoked potential

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Abstract Humans are able to distinguish eye movement-induced retinal image motion and physical object motion during smooth pursuit eye movements. We investigated the neurophysiological basis of this ability by comparing motion-onset visual evoked potentials (VEPs) to onset of: (1) physical object motion during fixation, (2) eye movement-induced retinal image motion, and (3) physical object motion during eye movements. Electro-oculographic (EOG) artifacts were removed and the influence of eye-movement quality was evaluated. Retinal image shift was of similar magnitude in all conditions (9°/s) and elicited typical motion-onset VEPs, with N2 at occipital and P2 at central derivations. During smooth pursuit, physical object motion induced N2 and P2 of higher latencies than during fixation. In the absence of physical object motion, i.e., for exclusively eye movement-induced retinal image motion, the N2 amplitude was reduced. This is taken as evidence that the activity of detectors of physical object motion is reflected by a part of the N2 component. N2 also reflects eye movement-induced retinal image motion. It is concluded that headcentric motion detection and the detection of eye movement-induced retinal image motion is mediated by brain mechanisms with similar latencies and, within the resolution limits of VEPs, at similar locations.

Keywords Cortex · Electro-oculography · Smooth pursuit · Eye movements · Human

Introduction

Smooth pursuit eye movements enable humans to track moving objects (reviewed by Ilg, 1997). Thus the objects are kept in the area of best spatial resolution, the fovea, and the retinal shift of their images is minimized. On the other hand, eye movements confront the visual system with a new problem, the distinction between eye movement-induced retinal image motion and physical object motion. Human oberservers can solve this problem and distinguish eye movement-induced retinal image motion from physical object motion, though they tend to make systematic errors known as the Filehne illusion (Filehne 1922; reviewed by Wertheim, 1994). In the present study, the ability to detect physical object motion despite ongoing eye movements will be referred to as headcentric motion detection. Headcentric motion detection requires quantitative knowledge about the eye movements, which could be based on retinal and extraretinal information (Wertheim 1994). The latter possibility is closely related to the efference copy concept (Helmholtz 1910; Sperry 1950; von Holst and Mittelstaedt 1950). Details of these mechanisms are still obscure and knowledge of their neural substrate is needed to uncover the underlying principles.

The neural substrate of headcentric receptive fields and headcentric motion detection has been addressed in a number of studies in macaque monkeys. Explicit headcentric receptive fields have been described only for higher visual areas such as the ventral intraparietal area (VIP; Duhamel et al. 1997; Gur and Snodderly 1997; Bridgeman 1999). Headcentric motion detection has been suggested for early visual areas (Galletti et al. 1984, 1988, 1990), but the explicit distinction between physical object motion and eye movement-induced retinal image motion is probably not accomplished before area MST (Fischer et al. 1981; Erickson and Thier 1991a, 1991b; Thier and Erickson 1992; Ilg and Thier 1996). Whether this also applies to the neural representation of headcentric motion detection in humans is unknown. Despite profound parallels between human and monkey visual cortex (Zeki et al. 1991; Sereno et al. 1995; Tootell and Taylor 1995; DeYoe et al. 1996; Tootell et al. 1996; Engel et al. 1997), it is still not known whether there is a human homologue of MST (Tootell et al. 1996). A recent case study supports the view that a local region in the occipitoparietal cortex

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M.B. Hoffmann · M. Bach (✉)
Elektrophysiologisches Labor, Universitäts-Augenklinik,
Killianstr. 5, 79106 Freiburg, Germany
e-mail: bach@uni-freiburg.de
Fax: +49-761-2704060

M.B. Hoffmann
Institut für Biologie I (Zoologie), Universität Freiburg,
Hauptstrasse 1, 79104 Freiburg, Germany

serves to distinguish between physical object motion and eye movement-induced retinal image motion in man, thus indicating a candidate for a human MST area (Haarmeier and Thier 1997). Furthermore, it has been shown in humans that visual-evoked potentials (VEPs) elicited by synchronous motion and pattern onset are affected by the actual strength of the perception of object motion (Haarmeier and Thier 1996), indicating a partial origin of this VEP component in the activity of a human MST homologue (Haarmeier and Thier 1998).

We here used the motion-onset VEP to investigate an electrophysiological correlate of the distinction between physical object motion and eye movement-induced retinal image motion in man. The motion VEP has long been used to study the neural substrate of human motion perception (MacKay and Rietveld 1968; Clarke 1972, 1973a, 1973b, 1974; Tyler and Kaitz 1977; Andreassi and Juszczak 1982; Göpfert et al. 1983; Kubovà et al. 1990; Bach and Ullrich 1994; Snowden et al. 1995). Visual motion-onset evokes VEP components at two sites: 1. Occipital and occipitotemporal sites (Oz and OT$_{1,2}$); 2. Central sites (Cz):

1. At occipital and occipitotemporal electrodes, a potential is evoked which is dominated by a positivity (P1, approx. 100–130 ms) and a negativity (N2, approx. 150–200 ms). These components have been studied thoroughly, as reviewed by Niedeggen and Wist (1998). The velocity- and contrast-dependence identified N2 as a motion-related component, whereas P1 is more likely to be associated with pattern processing (Markwardt et al. 1988; Müller and Göpfert 1988; Kubovà et al. 1990, 1995; Schlykowa et al. 1993; Bach and Ullrich 1997). Additionally, N2 is very susceptible to motion adaptation (Göpfert et al. 1983, 1984; Müller et al. 1985; Schlykowa et al. 1993; Bach and Ullrich 1994; Wist et al. 1994) and matches human motion perception in its time course of motion adaptation and recovery (Hoffmann et al. 1999). The direction specificity of motion adaptation implies that at least a quarter of the N2 amplitude reflects veridical motion processing (Bach and Hoffmann 2000; Hoffmann et al. 2001). Source analysis showed that N2 originates in or around the middle temporal area (MT; Probst et al. 1993). Hence N2 can be regarded as a component reflecting motion processing
2. At central electrodes (Cz), P2 with a latency of approx. 250 ms is evoked by visual motion-onset. Its amplitude depends on stimulus velocity (Hoffmann and Bach 1997a) and it is susceptible to motion adaptation; however, not in a direction-specific manner (Hoffmann et al. 2001). We conclude that P2 does not reflect veridical motion processing and must be attributed to other processes triggered by motion onset.

The aim of this study was to investigate whether headcentric motion detection and the detection of eye movement-induced retinal image motion activate brain mechanisms with similar latencies and locations in the brain. We addressed this issue with VEP measurements. To determine the contribution of the activity of headcentric motion detectors to the motion-onset VEP, we compared motion-onset VEPs to: (1) physical object motion during fixation, (2) eye movement-induced retinal image motion, and (3) physical object motion during eye movements. Preliminary accounts of this work have been presented previously (Hoffmann and Bach 1997b; Hoffmann 1998).

Methods

Subjects

VEPs were recorded from nine human observers with normal or corrected-to-normal visual acuity (at least 1.0). They gave their informed consent to participate in the experiment.

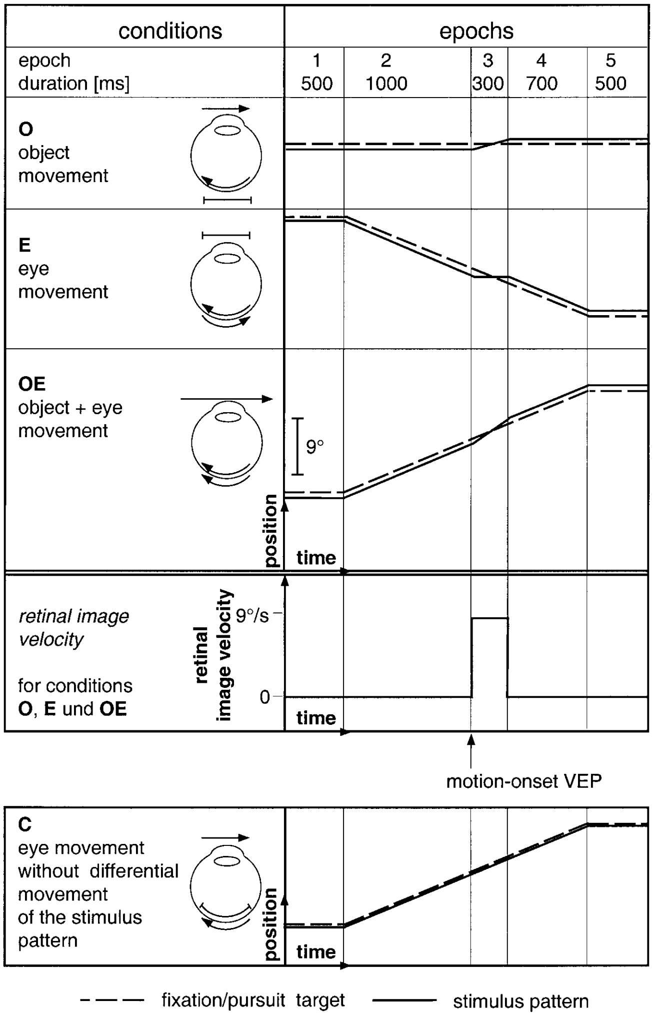

Fig. 1 The stimulus paradigm used to isolate the activity of headcentric motion detectors. The temporal sequence of the stimuli is subdivided into 5 epochs. Movement of pursuit target (eye; dashed) and stimulus object (solid) is indicated. Given that the observers pursue the pursuit target, there is an equal amount of retinal image shift in epoch 3 (300 ms; *shaded*) for stimulus conditions O, E, and OE. This is indicated in the second row from the bottom (retinal image velocity). Condition C is a control condition without retinal image shift, hence no motion-onset VEP is expected. While only stimulus conditions with leftward image shift are depicted here all conditions were also presented with rightward image shift

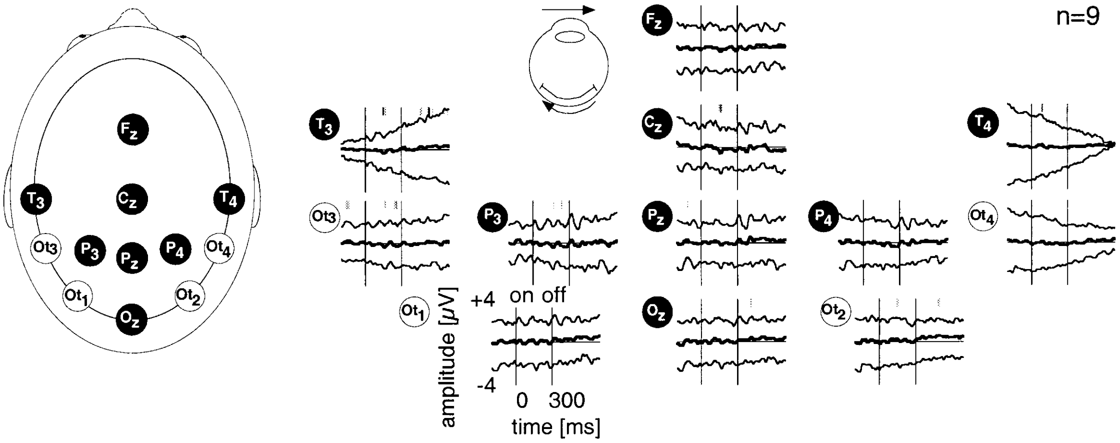

Fig. 2 VEPs for control condition C without retinal image shift recorded from 12 sites referenced to linked ears (see left inset: *filled circles* indicate use of 10–20 system, *open circles* indicate additional sites introduced for better sampling of motion-onset potentials). Traces are arranged according to recording sites. *Vertical lines* indicate the begin and end of retinal image shift in conditions O, E, and OE; no retinal image shift is expected to occur during this epoch in this control condition. *Thin traces* are responses during smooth pursuit to the left or right (displaced by ±2 μV to avoid overlap). EOG artifacts are most pronounced at temporal recording sites. *Thick traces* show the residual EOG artifact after averaging responses during smooth pursuit to the left and to the right. The significance level of the deviation of this trace from 0 μV is indicated *above the traces* with a grayscale code (*gray bars*: $P<0.05$; *black bars*: $P<0.01$). Condition C further served as a control to test whether the continuous movement of the gray screen on the retina (due to pursuit eye movements) elicits VEPs, which might interfere with the motion-onset VEPs to conditions O, E, and OE. Only small potentials are elicited by the eye movement. There is no overlap in time or topography with N2 (approx. 160 ms, especially at occipital, Oz, and occipitotemporal, Ot$_{1,2}$, sites) or P2 (approx. 250 ms especially at Cz) of the typical motion-onset VEP. Hence no influence on motion-onset VEPs is expected

Stimuli

Computer-generated stimuli were presented on a CRT, with a frame rate of 60 Hz, at a viewing distance of 57 cm. Experiments were conducted in a dark, black room to exclude motion of the image of the laboratory on the subject's retina during the execution of eye movements. Thus a better control of the stimulus conditions is achieved. The stimulus comprized a fixation mark/pursuit target (black cross on white square; size 2.5°×2.5°) and a stimulus pattern (size 9°×18°), which could move independently across the screen according to the respective stimulus condition. The stimulus was displayed on a gray screen (size 28°×23°) with equal luminances of screen and stimulus pattern (5 cd/m^2). The stimulus pattern consisted of random dots (element size 0.06°×0.06°; contrast 98%; 50% black and 50% white elements). The fixation/pursuit target was placed in the center of the stimulus pattern. One trial lasted 3 s. The motion epoch consisted of an abrupt onset of continuous, coherent retinal image motion for 300 ms at 9°/s either during fixation or during smooth pursuit (see section Paradigm and rationale).

Paradigm and rationale

We used four different stimulus conditions: O (physical object motion), E (eye movement-induced motion), OE (physical object motion during eye movements), and C (control). Each stimulus condition was presented for both motion directions, leftward and rightward. Stimulus conditions are summarized in Fig. 1: The temporal sequence was subdivided into 5 epochs; movement of pursuit/fixation target (eye) and stimulus object is indicated. Stimulus conditions are summarized as follows: One trial, encompassing 5 epochs, lasted 3,000 ms. In all conditions there was a period of 2,700 ms (epochs 1, 2, 4, and 5) with uniform motion of fixation/pursuit target (eye) and stimulus object. In the conditions O, E, and OE, there was a period of 300 ms (epoch 3) in which the movement of pursuit/fixation target (eye) and of stimulus object differed (Fig. 1, shaded area), entailing retinal image shift. This image shift evoked a motion-onset VEP in any of the conditions O, E, and OE. The motion-onset VEP was due to either physical object motion during fixation (condition O) or to eye movement-induced retinal image motion (condition E), or to physical object motion during eye movements (condition OE). Given accurate pursuit, retinal image shift of similar magnitude is induced during ongoing pursuit and fixation. With this paradigm, catch-up saccades accompanying smooth pursuit initiation are avoided, since in conditions E and OE retinal motion onset is induced during ongoing pursuit. Condition C served as a control: There was no difference in movement of pursuit target and stimulus object in this condition, hence no motion-onset VEP was expected. Therefore this condition allowed us (a) to assess whether the movement of the gray screen on the retina influenced the VEP, and (b) to evaluate the efficiency of the EOG artifact removal. Conditions O, E, and OE were chosen because they allow us to evaluate: (1) the influence of smooth pursuit eye movements on motion-onset VEPs (comparison of conditions OE and O); and (2) the impact of the origin of retinal image shift onset (physical or eye movement-induced) on the motion-onset VEP (comparison of conditions E and OE).

Procedure

Subjects stabilized their heads with a chin rest. Stimuli were presented in an interleaved block design. The three conditions O (physical object motion), E (eye movement-induced retinal image motion), and OE (physical object motion during eye movements) were presented in 8 blocks separated by short breaks. Each block consisted of a sequence of 24×E (rightward and leftward), 12×O (rightward and leftward), 24×OE (rightward and leftward), and 12×O (rightward and leftward). After each block, condition C (control; rightward and leftward) was presented 24 times; then the EOG was recalibrated. At least 85 trials for each condition and stimulus direction were averaged after rejection of artifacts and evaluation of eye movements. Experiments were conducted in darkness. In all, each session lasted about 3 h, including a break in the middle.

VEP and EOG recording

We recorded the horizontal EOG bitemporally to monitor eye movements and the vertical EOG of the right eye for blink detection. EOGs were amplified, filtered (0.001- to 23-Hz 1st-order

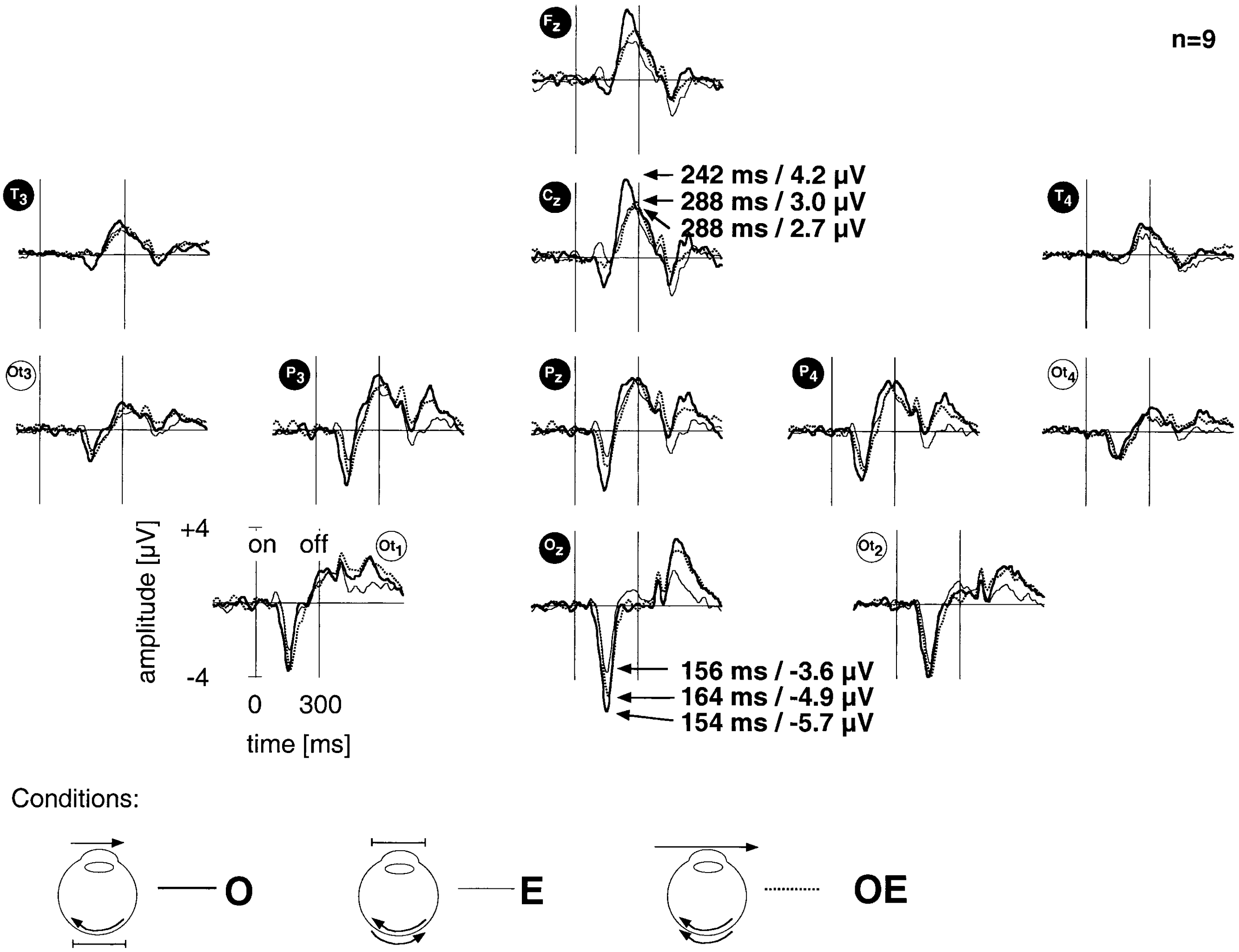

Fig. 3 VEPs to conditions O, E, and OE recorded from 12 sites (see inset in Fig. 2). Traces are arranged according to recording sites; *vertical lines* indicate begin and end of retinal image shift. In all three conditions a typical motion-onset VEP with P2 at Cz and N2 at Oz is elicited. While there is no difference in the topographic distribution of the VEPs between conditions O, E, and OE, P2 and N2 amplitudes and latencies do depend on the stimulus condition as indicated

low-pass filter) and digitized at a sampling rate of 500 Hz; the horizontal EOG was regularly recalibrated. VEPs were recorded from 12 electrodes referenced to linked ears (see inset in Fig. 2): 8 electrodes were placed according to the 10-20 system (Jasper 1958) and 4 electrodes were placed 5 cm and 10 cm left and right from Oz following previous motion-onset VEP studies. A ground electrode was attached to the right wrist. Signals were amplified, filtered (0.33- to 70-Hz 1st-order low-pass filter; Toennies Physiological Amplifier), and digitized at a sampling rate of 500 Hz.

Data analysis

Trials were analyzed from 200 ms before to 700 ms after motion onset. Trials with blinks, detected with a threshold criterion of 100 μV, were discarded off-line. The first two trials after a stimulus change were discarded. Averaged sweeps were digitally filtered (40-Hz low-pass). Baseline was defined as the mean value from –100 ms to +70 ms of the averaged trace and used as zero. Eye movements were evaluated with two criteria: (1) a velocity criterion, and (2) a position criterion.

1. Eye velocity was determined as the slope of the regression line fitted to the horizontal EOG in an analysis interval of 900 ms (200 ms before and 700 ms after motion onset). If this slope deviated by more than 2°/s from the target velocity (0°/s for condition O, 9°/s for conditions E, OE, and C), the trial was rejected
2. The position of the pursuit target was estimated with the regression line and the trial was rejected whenever eye and target position deviated by more than 2°.

Removal of the EOG artifact

During eye movements some crosstalk of EOG and EEG is expected (Brunia et al. 1989; Krieger et al. 1995). The effect was reduced using linked ears as reference, but there was still a small amount of EOG artifact left. For left- and rightward movement this artifact had the same magnitude but opposite sign, opening the possibility of cancelling it by averaging trials for leftward and rightward movement. Thus we removed the EOG artifact using a paradigm with one half of the eye movement trials to the left and the other half to the right.

Statistical analysis

To determine whether specific VEP components significantly differed from a potential of 0 μV, a running *t*-test was performed, which permits time-resolved statistics. However, the reader has to take into account that *P*-values are not corrected for multiple testing. In the figures, *P*-values are indicated in gray scales above the traces. Multiple testing has been taken into account for the evaluation of the VEP peak differences for the different stimulus conditions in Fig. 4. Here, normalized data were evaluated with an ANOVA and tested post hoc with the Student-Newman-Keuls test. Significance levels are indicated in Fig. 4 (*$P<0.05$; **$P<0.01$).

Results

Effect of smooth pursuit on the EEG

Figure 2 shows VEPs recorded during control condition C. EOG artifacts and their removal can be evaluated. There was no onset of retinal image motion of the stimulus during the interval of analysis: the eyes moved over the gray screen tracking pursuit target and stimulus object according to the scheme in Fig. 1. Vertical bars were inserted to indicate motion onset and offset in the stimulus conditions O, E, and OE used in the other experiments. The EOG artifact was removed by averaging responses during rightward and leftward smooth pursuit. Residual potentials were smaller than 0.6 µV at all times and derivations; due to their different latency and topography, they would not overlap with the typical motion-onset VEP (N2, P2). Therefore neither continuous motion of the image of the screen nor crosstalk of the EOG into the EEG are reflected in the motion-onset potentials to conditions O, E, and OE.

VEPs to onset of physical object motion and eye movement-induced retinal image motion

In Fig. 3 the responses to the three motion-onset stimulus conditions O, E, and OE are summarized. In all three conditions, motion-onset VEPs with the typical N2 (approx. 160 ms after stimulus onset) at occipital and occipitotemporal derivations and P2 (approx. 250 ms after stimulus onset) at frontal derivations were elicited. To a first approximation, VEPs to all conditions were similar, indicating a predominance of motion processing in retinal coordinates. In all three conditions, N2 and P2 amplitudes were maximal at Oz and Cz, respectively. A quantitative analysis of amplitudes and latencies revealed a dependence on stimulus conditions (Fig. 4): P2 was delayed during smooth pursuit (conditions E and OE), and N2 was delayed during smooth pursuit for the physical object motion condition only (OE). The differential effect of smooth pursuit on the N2 amplitude is of special interest: During exclusively eye movement-induced onset of retinal image motion (condition E), N2 amplitudes were reduced compared with onset of physical object motion (conditions OE and O). This is illustrated in Fig. 5 by the difference plots of the responses to the conditions E and OE, which yield the headcentric motion component. Furthermore, Fig. 5 shows not only that N2 is affected (amplitude reduction at 176 ms by 1.8 µV), but also that later responses, after approx. 300 ms, are reduced (by 1.2 µV). These amplitude reductions are maximal at occipital and occipitotemporal electrodes, respectively. Finally, there is a significant positivity after the offset of motion, which is very likely to be associated to eye movements deviating from smooth pursuit as will be discussed in a later section (Fig. 6).

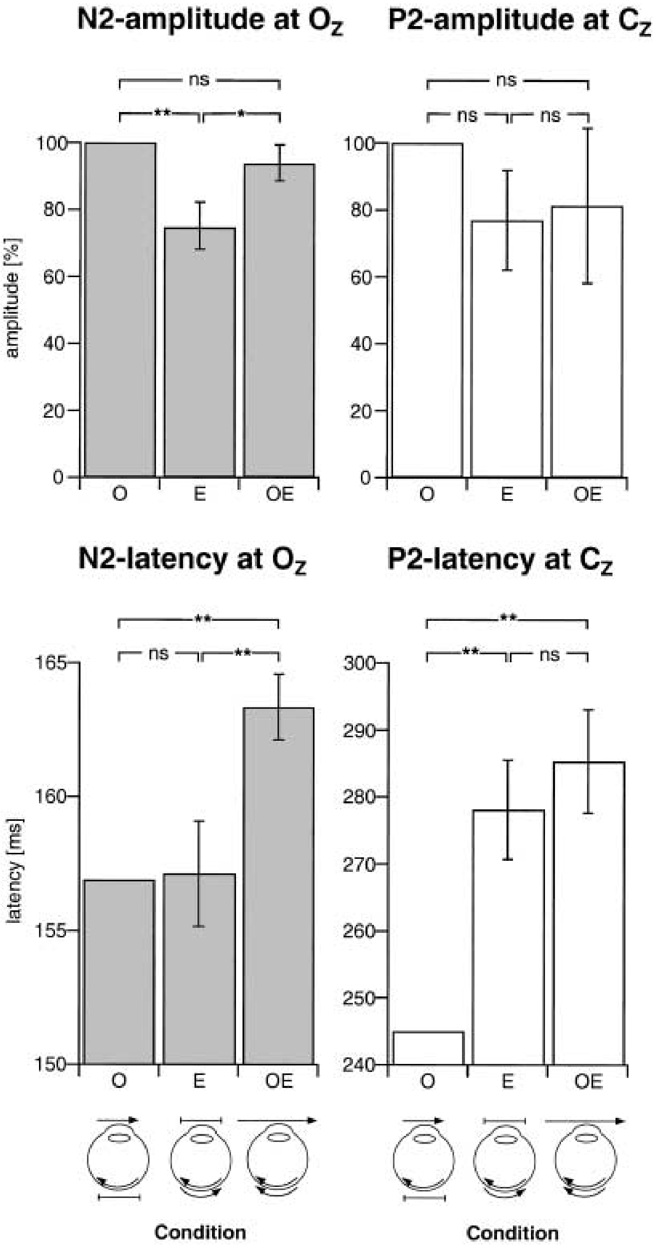

Fig. 4 Effects of stimulus conditions O, E, and OE on N2 and P2 amplitudes and latencies at Oz and Cz, respectively. Values were determined from peaks of the individual subjects (means ± SEM; $n=9$) and normalized with respect to condition O: Amplitudes were devided by baseline amplitudes, from the latencies the reference latencies (condition O) were subtracted. Mean reference latencies were added to the normalized mean latencies to indicate their actual magnitude. During smooth pursuit (conditions E and OE), P2 latencies are prolonged. Effects on N2 amplitude and latency depend on the content of physical object motion in the stimulus (condition E vs OE)

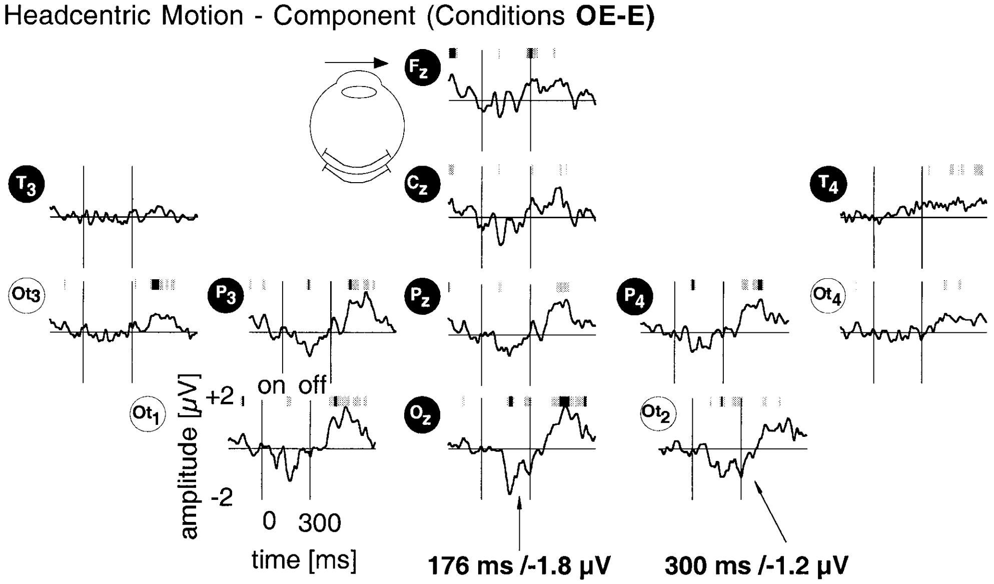

Fig. 5 Difference traces of the VEPs to conditions OE minus E, resulting in the headcentric motion component (conventions as in Figs. 2 and 3). The significance of the difference of the traces from zero is indicated *above the traces* with a grayscale code (*gray*: P<0.05; *black*: P<0.01). Conditions OE and E differ only in the degree of physical object motion, hence the difference of the responses should isolate the activity of a headcentric motion detector, termed headcentric motion component. This headcentric motion component is indeed found and consists of two negativities, one after 176 ms at Oz and one approx. 300 ms at OT_2

Eye movements

Figure 6a depicts the mean eye velocity during conditions O, E, and OE and during control condition C and thus allows one to assess the quality of the eye movements in the respective conditions. While these plots do not permit the identification of source of pursuit/fixation inaccuracies (changes in pursuit velocity or small saccades), they do permit the assessment the mean quality of mean fixation and pursuit as such. During fixation (condition O), eye movements are almost unaffected by motion onset of the stimulus, whereas they are strongly affected during pursuit: The mean eye velocity has the tendency to converge toward that of the stimulus pattern, entailing a decrease in mean eye velocity in condition E and an increase in condition OE.

The influence of these eye-movement inaccuracies on the motion-onset VEP was evaluated as follows: We compared VEPs from trials with eye movements of different precision. VEPs during eye movements of (a) “below median accuracy” and (b) “above median accuracy” eye movements. For each subject these two classes of eye movements were obtained with the following procedure: (1) for each trial the maximal deviation of eye position from target position was determined for the interval of 50–250 ms after motion onset; (2) the median of the eye-position deviations was determined; (3) trials were then grouped into two classes: Trials in which the eye position converged stimulus position more than for the median eye-position deviation were grouped as trials with eye movements below median accuracy. Trials in which the convergence was smaller than the median were grouped as trials with eye movements above median accuracy. The resulting EOG traces are depicted in Fig. 6b. An important issue is whether grouping the eye movements according to this scheme is simply dividing noise from noise. Figures 6b and 7 show that this is clearly not the case: (a) the two groups of eye movements do not only differ in the time window used to distinguish between the two groups, but also at greater latencies; (b) the two groups also differ in the independent measure, the resulting VEPs.

Figure 7 demonstrates the effect of smooth pursuit quality on the motion-onset VEP. In condition E the motion-onset VEP was strongly affected by the precision of smooth pursuit (Fig. 7a). In the case of below-median-accuracy eye movements, i.e., with big excursions from smooth pursuit, there was (1) an additional early component approx. 120 ms at nonoccipital electrodes (around Cz); and (2) a reduced P2 of approx. 300 ms, especially at occipital and parietal derivations. The occipital N2, however, was not affected by smooth pursuit precision. This is also reflected by part of the headcentric motion component elicited by physical object motion (Fig. 7b): The negativity at approx. 300 ms depends on the precision of the eye movements, it is enhanced in the case of below-median-accuracy eye movements. In contrast, the occipital negativity at approx. 160 ms is not affected by the precision of smooth pursuit after motion onset. Therefore this component is very likely to arise from the different origin of the onset of retinal image motion (eye-induced image motion vs physical object motion) in conditions E and OE, which makes it a candidate for an electrophysiological correlate of headcentric motion detection.

Discussion

Abrupt onset of motion elicits typical motion-onset VEPs during both fixation and smooth pursuit eye movements. The topographic distribution of N2, i.e., the negativity of approx. 160 ms, and P2, i.e., the positivity of approx. 250 ms after stimulus onset, is similar for the different stimulus conditions; amplitudes and latencies, however, were affected by smooth pursuit. The VEP component which is presumably due to the activity of headcentric motion detectors can be extracted by subtracting the VEP to condition E from that to condition OE (see Methods, Paradigm and rationale). This revealed two negativities with different latencies, approx. 175 ms and 300 ms. Further analysis of the influence of eye-movement deviations showed that the early component (approx. 175 ms) is not significantly influenced by eye-movement deviations during smooth pursuit, whereas the later component (approx. 300 ms) is. We conclude that the early component is a candidate for a VEP correlate of headcentric motion detection. This “headcentric motion component” is part of N2 of the common motion-onset VEP. Therefore the entire N2 arises from three mechanisms at least: Hoffmann and coworkers have already decomposed N2 into two parts, one due to a direction-specific and another due to a non-direction-specific mechanism (Hoffmann et al. 2001). Here we show that the direction-specific part of N2 might again be attributed to two mechanisms: (1) a motion detector that can distinguish between physical object motion and eye movement-induced retinal image motion, namely a headcentric motion detector; and (2) a motion detector that cannot distinguish between these two types of motion. The overlap of the headcentric motion component and the eye movement-induced motion VEP in time and topography suggests that headcentric motion detection and the detection of eye movement-induced retinal image motion are mediated by brain mechanisms with similar latencies and with similar locations in the brain. This prompts the question whether these components still arise from two distinct visual areas, as in the macaque monkey (MT and MST). In the macaque monkey, areas MT and MST are adjacent and, despite different response dynamics, the latencies of their neurons do not differ by more than 10 ms (Lagae et al. 1994; Ferrara and Lisberger 1997). Consequently responses of these two areas could well merge into the same VEP component.

Comparison with other VEP studies

The first to investigate perception of physical object motion with VEPs were Haarmeier and Thier (1998). They

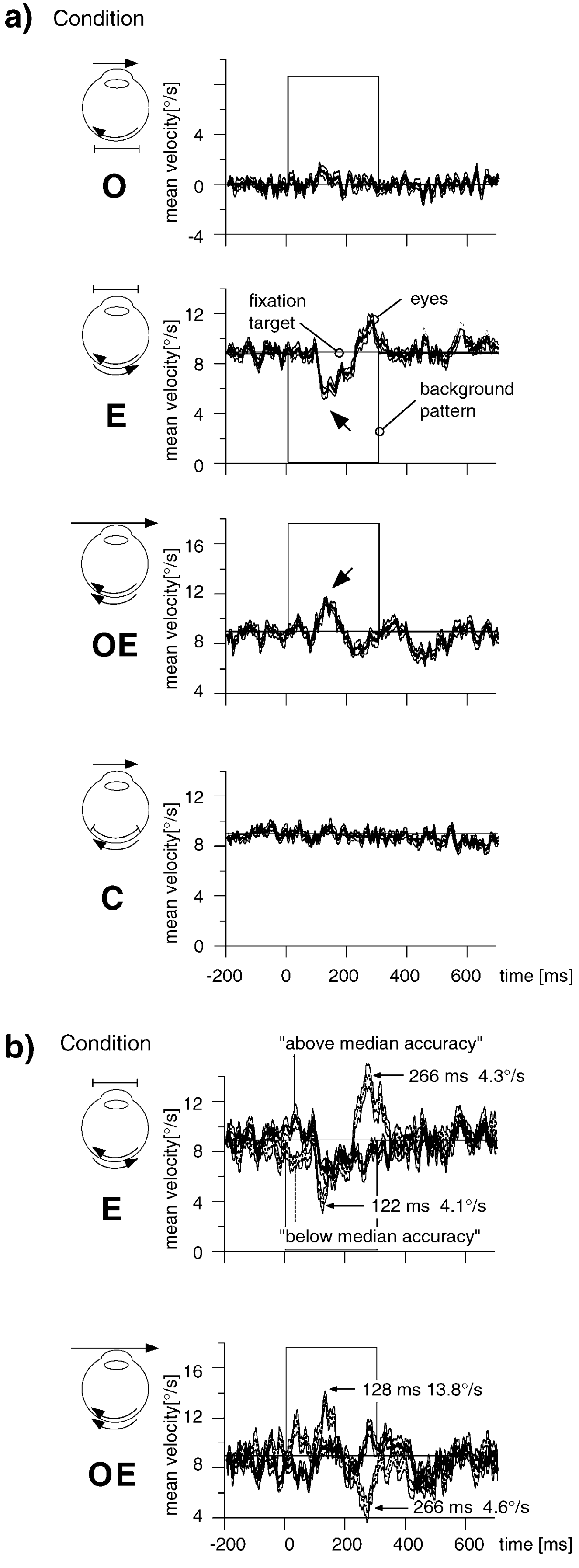

Fig. 6a, b Velocity of eye movements during conditions O, E, OE, and C. EOGs were averaged over trials and subjects to inrease resolution. **a** Condition C serves as a control without retinal image shift, hence without disturbance of eye movements. During fixation (condition O) retinal image shift has only little effect on eye-velocity. In contrast, there is a strong influence of retinal image shift on eye-velocity during smooth pursuit: eye velocity converges toward the velocity of the stimulus object. Hence the eyes decelerate in condition E and accelerate in condition OE. **b** Eye velocities during conditions E and OE, grouped into two classes: eye movements “above median accuracy” and “below median accuracy.” Depending on their precision (see text) eye movements were grouped into two classes. For both conditions, E and OE, the eye movements of the two classes differ considerably

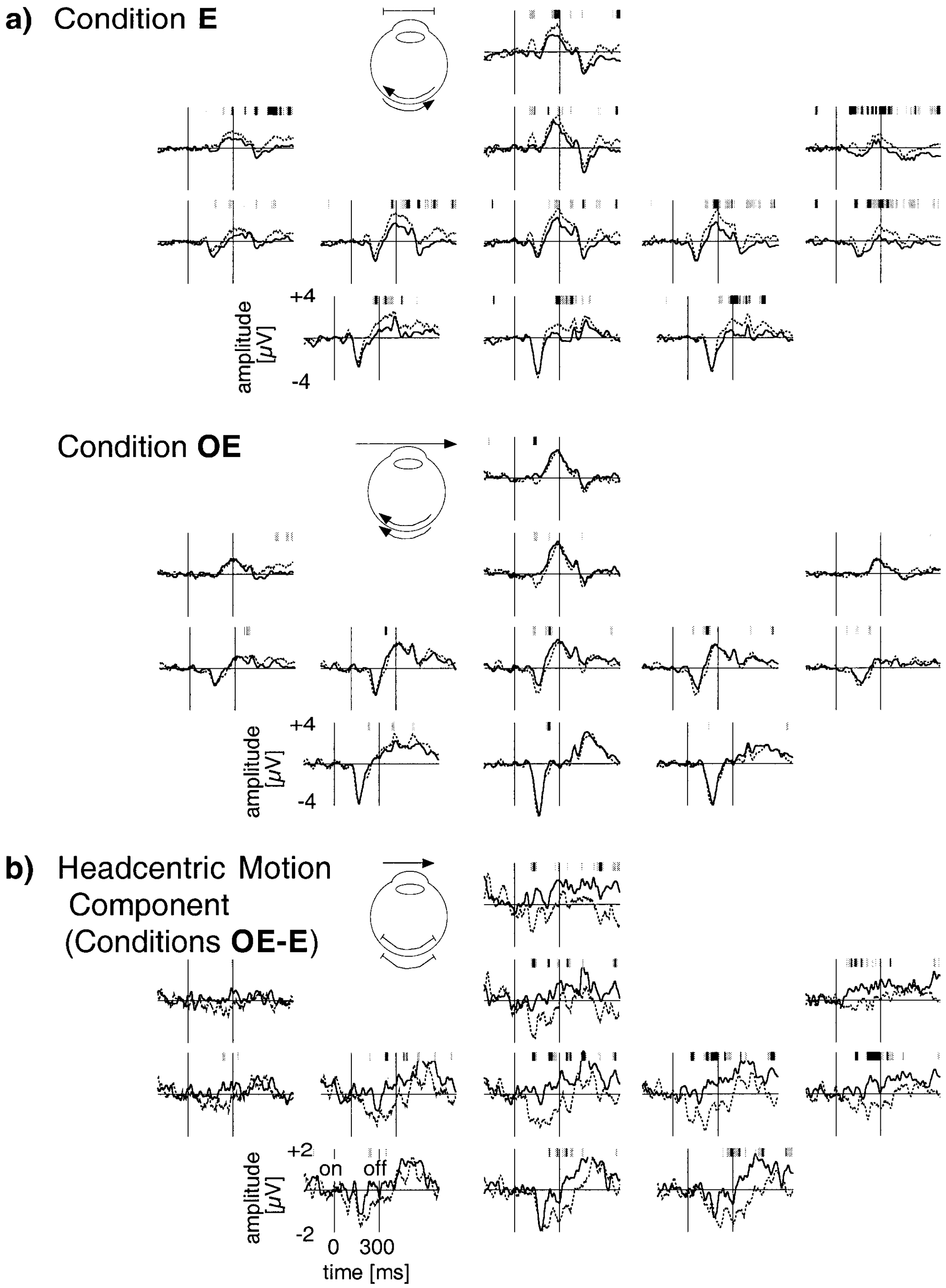

Fig. 7a, b VEPs to conditions E and OE in (a) and the resulting headcentric motion component (condition E subtracted from condition OE) in **b** for trials with “above median accuracy” (*solid trace*) and “below median accuracy” (*dashed trace*) eye movements (conventions as in Figs. 2 and 3). The significance of the difference between the two traces is indicated *above the traces* with a grayscale code (*gray*: $P<0.05$; *black*: $P<0.01$). Scales differ in **a** and **b**. **a** Eye-movement precision affects the VEP, especially in condition E: (1) There is an additional component at Cz after approx. 120 ms; (2) P2 is reduced at all derivations. N2, however, is not affected by the precision of the eye movements. **b** The headcentric motion component is partially affected by eye-movement deviations during smooth pursuit: The late headcentric motion component (approx. 300 ms) is markedly affected, whereas the early headcentric motion component, approx. 170 ms, at occipital and occipitotemporal electrodes is not significantly affected

found the amplitude of a negative component of approx. 300 ms (N3) to depend on the strength of the Filehne illusion; with increasing perceived object motion the amplitude of this component increased. In this respect their finding corresponds with ours that the N2 amplitude increases in the presence of physical object motion. However, as their component has a latency of approx. 300 ms, it contrasts with our finding of a headcentric motion component as early as the N2. As Haarmeier and Thier evaluated only trials with high-precision pursuit eye movements, eye-movement artifacts are an unlikely source of the discrepancy of the results. Interestingly, Kleiser and Skrandies (2000) found both an early and a late VEP component related to headcentric motion detection when they investigated motion perception during saccades. They described comparatively short latencies of these two components, 140 ms and 220 ms, which can be attributed to the substantially higher stimulus velocities they used (minimum 175°/s). Thus the components they describe are likely to be equivalents of the N2 and N3 changes found in the present study and the study by Haarmeier and Thier, respectively. Currently we do not know what the differences between the early and late components are.

Influence of eye movements on the VEP

Smooth pursuit eye movements are affected by structured background (Yee et al. 1983; Keller and Khan 1986; Kimmig et al. 1992; Mohrmann and Thier 1995; Haarmeier and Thier 1996; Schwarz and Ilg 1999; Suehiro et al. 1999). A detailed analysis of the influence of eye movement inaccuracies on motion-onset VEPs showed the following: (1) An early frontal component associated with deviations from smooth pursuit slightly preceded the eye movement deviations (118 ms vs 122 ms); (2) N2 at occipital and occipitotemporal derivations is unaffected by these deviations; (3) later components (approx. 300 ms) at these derivations are affected. Due to its small latency, the early frontal activity might be associated with the neural activity preceding, possibly causing, the deviations from smooth pursuit. This is supported by its topographic distribution, which suggests generators in the frontal areas, possibly the frontal eye fields, which are involved in the generation of eye movements (Goldberg and Segraves 1989; Petit and Haxby 1999). Later components linked to deviations from smooth pursuit are preceded by eye movement inaccuracies of approx. 170 ms earlier and might be due to retinal image shifts induced by these eye-movement inaccuracies. The eye-movement dependent VEP components can therefore be attributed to both planning activity and retinal image shift. The main finding, however, is that the N2 at occipital and occipitotemporal electrodes is not affected by the deviation of the eyes from smooth pursuit. This is discussed in detail in the following paragraph.

Pursuit velocity changes as an artifact source

The stimulus conditions O, E, and OE differ not only in the origin of the retinal motion onset, but also in their influence on mean pursuit velocity. Therefore differences in the retinal image slip might be induced which could account for the differences in the N2 component we report. This needs to be assessed carefully, and a consideration of the latencies of VEPs and pursuit velocity changes shows that the additional retinal image slip is unlikely to affect the N2 component: Eye-velocity changes peak at approx. 125 ms, while N2 peaks at approx. 160 ms after stimulus onset. This leaves only 35 ms for the pursuit velocity-induced retinal signal to evoke a secondary VEP on top of the one evoked by the main motion-onset stimulus, an epoch which is clearly too short to evoke a VEP under our experimental conditions (Bolz et al. 1982; Raiguel et al. 1989). Further evidence to support this point can be taken from our analysis based on the distinction of two classes of eye-movement precision: The VEPs to stimulus conditions E and OE at occipital recording sites are influenced by eye-movement precision only at latencies of more than 200 ms, i.e., the N2 is not affected by pursuit quality. This strongly supports the latency consideration discussed above. We conclude that we can assess the influence of the different stimulus conditions on components with a latency of less than 200 ms, i.e., on N2, and that we cannot assess the influence for components with a latency of more than 200 ms, i.e., following N2, such as P2 or the motion offset component, as they might be influenced by retinal image slip induced by pursuit-velocity changes.

Filehne illusion

For the interpretation of the headcentric motion component, the Filehne illusion must be considered. In condition E there is no physical object motion, but subjectively object motion can be perceived, which is known as the Filehne illusion (Filehne 1922): The subject perceives a small amount of object motion during smooth pursuit, although the object is physically stationary. Are there any implications of the Filehne illusion for the headcentric motion VEP investigated in the present study? The headcentric motion VEP has been extracted as the *difference* between the responses to conditions E and OE, i.e., conditions with *no* headcentric motion and with headcentric motion, respectively. However, the percept of the Filehne illusion introduces a small headcentric motion component into the response to condition E. Thus the headcentric motion signal induced by the Filehne illusion in condition E would be subtracted from the stimulus-induced headcentric motion signal in condition OE. Consequently, the percept of the Filehne illusion is expected to reduce the headcentric motion VEP. Indeed, it should be expected that reducing the strength of the Filehne illusion by a compensatory movement of the stimulus pattern should enhance the headcentric motion component. Evidence from Hoffmann (1998) indicates that this might actually be the case.

It is unlikely that possible illusory percepts concerning relative motion between screen border and stimulus pattern which have been reported previously (Mesland and Wertheim 1996) confound the interpretation of the headcentric motion VEP in our experiment, as we obtained this VEP component also when the screen borders were invisible, because we presented the stimulus pattern on a dark screen (Hoffmann 1998).

Typical motion-onset VEPs with a similar topographic distribution are elcited during both physical object motion and eye movement-induced retinal image motion. The N2 amplitude is reduced in the absence of physical object motion. It is concluded that part of the N2 reflects the activity of headcentric motion detectors and therefore represents a candidate for an electrophysiological correlate of headcentric motion detection. The fact that both physical object motion and eye movement-induced retinal image motion contribute to the N2 component of the motion-onset VEP suggests that headcentric motion detection and the detection of eye movement-induced retinal image motion are mediated by brain mechanisms with similar latencies and with similar locations in the brain.

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