J Neurophysiol 101: 2317–2327, 2009.
First published March 11, 2009; doi:10.1152/jn.91248.2008.

Chromatic Contrast Sensitivity During Optokinetic Nystagmus, Visually Enhanced Vestibulo-ocular Reflex, and Smooth Pursuit Eye Movements

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Submitted 24 November 2008; accepted in final form 3 March 2009

Schütz AC, Braun DI, Gegenfurtner KR. Chromatic contrast sensitivity during optokinetic nystagmus, visually enhanced vestibulo-ocular reflex, and smooth pursuit eye movements. *J Neurophysiol* 101: 2317–2327, 2009. First published March 11, 2009; doi:10.1152/jn.91248.2008. Recently we showed that sensitivity for chromatic- and high-spatial frequency luminance stimuli is enhanced during smooth-pursuit eye movements (SPEMs). Here we investigated whether this enhancement is a general property of slow eye movements. Besides SPEM there are two other classes of eye movements that operate in a similar range of eye velocities: the optokinetic nystagmus (OKN) is a reflexive pattern of alternating fast and slow eye movements elicited by wide-field visual motion and the vestibulo-ocular reflex (VOR) stabilizes the gaze during head movements. In a natural environment all three classes of eye movements act synergistically to allow clear central vision during self- and object motion. To test whether the same improvement of chromatic sensitivity occurs during all of these eye movements, we measured human detection performance of chromatic and luminance line stimuli during OKN and contrast sensitivity during VOR and SPEM at comparable velocities. For comparison, performance in the same tasks was tested during fixation. During the slow phase of OKN we found a similar enhancement of chromatic detection rate like that during SPEM, whereas no enhancement was observable during VOR. This result indicates similarities between slow-phase OKN and SPEM, which are distinct from VOR.

INTRODUCTION

Primates equipped with a foveal region of high acuity are able to stabilize their gaze continuously by different kinds of tracking eye movements depending on their own behavior, their surround, and their interest. These slow eye movements help to avoid blurred retinal images of the foveated objects even during locomotion or head movements. Depending on the type of motion, i.e., local object motion or large field movement, different neural pathways initiate these tracking eye movements (see Ilg 1997; Leigh and Zee 1999 for overviews): smooth pursuit eye movements (SPEMs) are elicited by the perception of motion of objects, whose images stimulate the foveal- or parafoveal retina. They are executed voluntarily and are used to keep the line of sight continuously on the selected moving target like a flying soccer ball or a running dog.

Whereas SPEM are present only in primates (Büttner and Büttner-Ennever 1988; Paige 1994), the optokinetic nystagmus (OKN) is found in all mammals and is the phylogenetically older system. The OKN is elicited during sustained self-rotation or by motion of a large part of the visual field or experimentally by rotating large patterns or stripes as in optokinetic drums. OKN consists of two distinct alternating phases: *1*) the *slow phase*, with smooth compensatory eye movements in the direction of motion; and *2*) the *fast phase*, with rapid eye movements in the direction opposite to the slow phase to reposition the eyes in the shortest time possible. At least two subtypes of OKN can be distinguished, depending on the instruction and behavior of the observer: a stare-nystagmus and a look-nystagmus (Ter Braak 1936). The *stare-nystagmus* consists of high-frequency fast phases and shorter slow phases and is present when the subject is asked to stare straight ahead and to "passively" perceive, for example, the moving drum stripes. The *look-nystagmus* consists of low-frequency fast phases and longer slow phases; it occurs when the subject is instructed to actively follow a selected drum stripe with his eyes.

The vestibulo-ocular reflex (VOR) is independent of visual stimulation and is elicited by head movements even in the dark. Gaze stabilization by the VOR is very important during all kinds of locomotion, which often results in changes of head position or continuous perturbations. Clear vision during walking, for example, is possible only because the VOR is fast enough to generate compensatory eye movements (Grossman et al. 1988, 1989). Acceleration sensors of the labyrinth signal head perturbations much sooner than it would be possible for the visual system to detect the resulting retinal motion. As a consequence VOR eye movements can occur at ultrashort latencies of $<$16 ms (Leigh and Zee 1999), which are not possible for visually guided eye movements. These three types of slow eye movements coexist and are often used in conjunction to stabilize gaze and to recognize and to interact with objects in a dynamic environment (Leigh et al. 1987; Paige 1983; Yee et al. 1983).

In general, gaze stabilization has two perceptual advantages that relate to retinal processing: first, retinal motion is minimized, which reduces image blur, and second, objects of interest are projected on the fovea, which increases the spatial acuity. Besides these direct retinal advantages it is known that slow continuous eye movements also exhibit more subtle influences on visual perception. Bedell and colleagues showed nicely that the extent of perceived motion smear is reduced during SPEM selectively for motion in a direction opposite to the eye movements (Bedell and Lott 1996; Tong et al. 2005, 2007). Interestingly, a similar attenuation is found during VOR (Bedell and Patel 2005) and inhibition of VOR (Tong et al. 2005). We recently showed that the sensitivity for both flashed color and high-spatial frequency luminance stimuli is enhanced during SPEM (Schütz et al. 2008). This enhancement precedes the onset of SPEM by about 50 ms, which suggests that an extraretinal signal actively triggers the enhancement.

In the present study, we investigated whether a similar enhancement of chromatic sensitivity is also present during

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two other types of slow eye movements: OKN and VOR. We chose OKN and VOR because they can cause similar eye-in-head movements as SPEM, but their input signals are rather different. OKN and VOR are also thought to be evolutionarily older and more reflexive than SPEM (Walls 1962). Doing so, we might gain new insights about the underlying mechanism for the chromatic improvement during SPEM and the neural basis for these different types of eye movements.

METHODS

Experiment 1: optokinetic nystagmus

SUBJECTS. One of the authors (ACS) and five naïve subjects participated in the experiment in which we measured chromatic detection rate. The naïve subjects were students of the Justus-Liebig University and were paid for their participation. Two naïve subjects and one of the authors (ACS) performed a control experiment to measure luminance detection.

EQUIPMENT. Subjects were seated in a dimly lit room facing a 21-in. CRT monitor (ELO Touchsystems, Fremont, CA) driven by a Nivida Quadro NVS 285 graphics board with a refresh rate of 100 Hz noninterlaced. At a viewing distance of 47 cm, the active screen area subtended 45° in the horizontal direction and 36° vertical on the subject's retina. With a spatial resolution of 1,280 × 1,024 pixels, this results in 28 pixels/deg. The subject's head was fixed in place using a chin rest.

EYE MOVEMENT RECORDING. Eye position signals were recorded with a head-mounted, video-based eye tracker (EyeLink II; SR Research, Osgoode, Ontario, Canada) and were sampled at 250 Hz. Subjects viewed the display binocularly. Stimulus display and data collection were controlled by a PC.

VISUAL STIMULI. To elicit OKN, we then presented a random-dot pattern, moving at 21.1°/s for 30 s. The random-dot pattern consisted of black dots with a diameter of 0.1°, which were presented on a uniform gray background. The average dot density of the pattern was 1 dot/deg^2. Two horizontal stripes were spared from the random-dot pattern: these stripes were located 2° above or below the vertical screen center and were 1° high. To measure detection rate, we flashed horizontal lines with a fixed contrast in red-green Derrington–Krauskopf–Lennie (DKL) color (Derrington et al. 1984) or in luminance within one of these stripes (Fig. 1). The DKL-color space consists of three axes: two axes correspond to the red-green and blue-yellow color opponent channels in the lateral geniculate nucleus and the third axis corresponds to the bright–dark luminance opponency. The line spanned the whole screen width and was vertically modulated by a Gaussian distribution with SD of 0.15°. It was flashed for one refresh cycle of the monitor. At a refresh rate of 100 Hz, this gives a nominal stimulus duration of 10 ms. Due to the decay of phosphors and sequential drawing, the actual stimulus duration was shorter. Measurement of the stimulus intensity with a photodiode showed that our phosphors decayed to 50% of peak in <1 ms and to 5% of peak in <2 ms. By using a line that was parallel to stimulus motion and by flashing it for just a brief period of time, we wanted to make sure that no retinal image motion would be induced by the eye movements.

EXPERIMENTAL PROCEDURE. At the beginning of each trial a black bull's-eye with an outer radius of 0.3° and an inner radius of 0.075° appeared at the screen center. The subjects had to fixate the bull's-eye and press an assigned button to start the trial. With pressing the button, the EyeLink II System performed a drift correction to correct errors of headband slippage or other factors. If the drift correction succeeded, the bull's-eye disappeared, so that no fixation point was present during the trial. Subjects were instructed to look at the moving random-dot pattern, without tracking an individual dot, and to indicate the position of the flashed line (i.e., top vs. bottom). After a buildup period of 2 s, where no lines were presented, we showed seven lines separated by pseudorandom intervals of ≥1.6 s and at most 4.8 s. At the same time as the lines, we presented 100-Hz tones for 10 ms, which signaled the subject to give his judgment about the location of the line. Fixation trials were exactly the same, except that the random-dot pattern remained stationary on the screen. Fixation and OKN trials were presented interleaved, with a ratio of 1:4. Color and luminance conditions were presented in different sessions.

EYE MOVEMENT ANALYSIS. To detect the fast-phase onset, we used the EyeLink saccade detector, which uses a combined velocity threshold of 22°/s and acceleration threshold of 4,000°/s^2.

PSYCHOPHYSICAL DATA ANALYSIS. We presented a line with a fixed contrast in red-green DKL color (Derrington et al. 1984), or in luminance, and analyzed the ratio of hits versus misses. The contrast level was determined for each subject individually to a 75% detection rate during fixation. We assumed that the time relative to the onset of the fast phase is a major factor influencing visual sensitivity. Thus we aligned the data to the preceding fast-phase onset, if the interval to the following fast phase was >100 ms or if the interval to the following fast phase was larger than that to the preceding fast phase. We excluded presentations that were not followed by a perceptual response within 1,000 ms (5%). Furthermore, we excluded presentations in which the vertical eye position at the time of line presentation was not between the two stripes that contained no random dots (8%). We also excluded cases in which the fast-phase amplitude was in the same direction as the motion direction (28%). Fast phases in motion direction were quite distinct from the usual fast phases against motion direction. Their average horizontal amplitude was much smaller (0.7° in motion direction vs. 6.5° against motion direction) and their latency to the preceding fast phase was also 100 ms smaller. Because the dots of our random-dot pattern had an unlimited lifetime, it might be that the subjects sometimes tried to track single dots, which might result in such small fast phases in motion direction. For analysis of the response latency we included only correct responses. To analyze the detection rate over time, we used a sliding histogram with a Gaussian weighting function, similar to a method used previously (Schütz et al. 2007a). To analyze the response latency over time, we used a weighted sliding average, again with a Gaussian weighting function.

Experiment 2: visually enhanced vestibulo-ocular reflex

EQUIPMENT. To allow the subjects to move their head freely, we did not use a chin rest in this experiment.

EYE MOVEMENT RECORDING. We switched off the eye tracker correction for head movements during the trials. As a consequence, we did not measure eye movements in space coordinates, but in head coordinates. Because we instructed the subjects to rotate their head, while fixating a central, stationary spot, we implicitly assumed that the eye-in-space position is always at the fixation spot and that the measured eye-in-head motion is determined primarily by the head movements. The eye-in-head position was used to determine the turning point for the horizontal head rotation and the onset of the line stimulus.

VISUAL STIMULI. In this experiment we used the same line stimulus as that in *experiment* 1. It was flashed for 10 ms, 2° above or below the fixation spot on an otherwise gray monitor screen.

EXPERIMENTAL PROCEDURE. At the beginning of each trial, the same drift correction as that in the OKN experiment was performed. In this experiment we used a bull's-eye only in fixation trials, in which subjects were required to hold their head stationary. In VVOR trials subjects were asked to fixate a small triangle pointing to the left or to the right. The triangle indicated the direction of the required head movement. After a successful drift

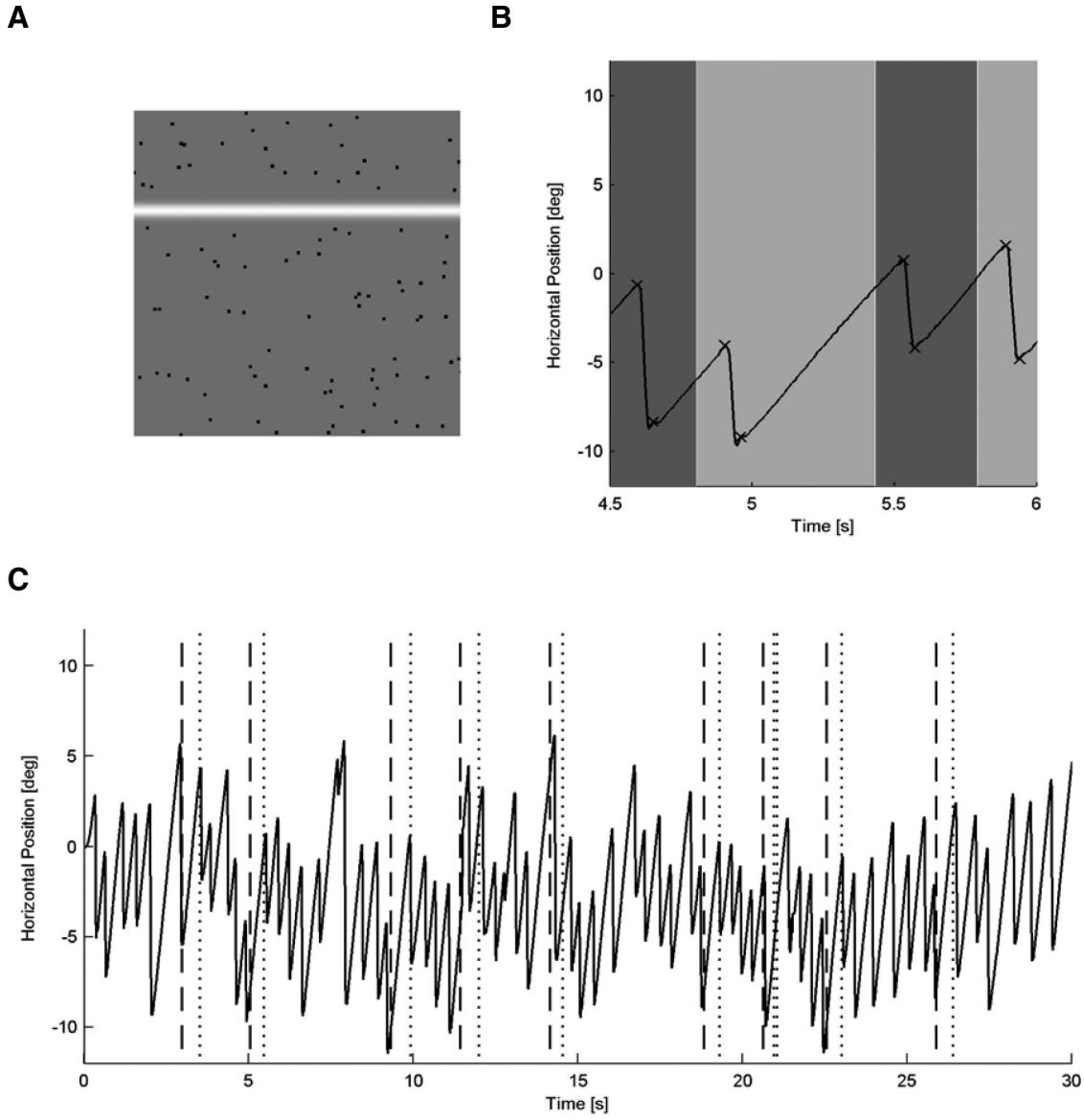

FIG. 1. *Experiment* 1: stimulus and sample eye traces. *A*: optokinetic nystagmus (OKN) stimulus display with line. *B*: detail of an exemplary eye trace. The continuous black line represents the horizontal eye position; fast-phase on- and offsets are marked by black crosses. The shaded regions indicate the time windows of the alignment to the nearest fast-phase onset: all line onsets that occurred in one of the time windows were aligned to the fast-phase onset in this time window. *C*: example eye trace of a complete 30-s trial. The dashed lines represent the line onsets and the dotted lines represent the subject responses.

correction, a black bull's-eye with an outer radius of 0.3° and an inner radius of 0.15° appeared at the center of the screen. In VVOR trials, subjects were required to rotate their head in the direction indicated by the triangle. To restrain the head movement, we provided the subjects with two acoustical references. As soon as the eye-in-head position exceeded 11.25°, a 100-Hz tone was given for 10 ms. The subjects were instructed to change the rotation direction right after the first tone and to go on with the rotation until the second tone occurred. The second beep occurred as soon as the eye-in-head position exceeded 11.25° in the opposite direction. In that way, subjects completed approximately 3/4 cycles of a sinusoidal rotation. We presented the line after the first beep, as soon as the eye-in-head position amounted to 4°. Only trials were used in which the subject's eye-in-head position traveled within 3 s from the center to 11.25° eccentricity on one side and to 11.25° eccentricity on the other side (95%). In fixation trials, subjects were required to stabilize their head and to fixate the bull's-eye for 1.5 s. We presented the horizontal line 1 s after trial onset. Color and luminance conditions were presented interleaved.

EYE MOVEMENT ANALYSIS. To detect saccades, we used the EyeLink saccade detector, which operates on a combined position and velocity criterion. We analyzed the eye-in-head movements in a 200-ms interval centered on the stimulus presentation. In this interval we calculated the average eye-in-head velocity. Trials in which a saccade occurred in this interval were excluded from further analysis (17%). Moreover, we excluded trials in which the vertical eye-in-head position exceeded an eccentricity of 2° (4%).

PSYCHOPHYSICAL DATA ANALYSIS. We determined on-line the line's contrast by an adaptive 2:1 staircase procedure (Levitt 1971) and used the psignifit toolbox to fit psychometric functions off-line (Wichmann and Hill 2001).

Experiment 3: fast smooth pursuit eye movements

If not stated otherwise, the methods are the same as those in *experiment* 2.

EQUIPMENT. As in *experiment* 1, the subject's head was fixed in place using a chin rest.

EXPERIMENTAL PROCEDURE. In fixation trials we presented the bull's-eye for 1,500 ms at the center of the screen, where observers had to keep fixation. At 1,000 ms after the beginning of the trial, we flashed the respective stimulus for 10 ms, 2° above or below the bull's-eye. In pursuit trials, we presented the bull's-eye at 10.6 or 18.5° left or right of the center of the screen, depending on the pursuit velocity and direction. After 250 ms, the bull's-eye moved toward the screen center at a velocity of 14.1 or 24.7°/s and subjects were instructed to track it as accurately as possible. When the bull's-eye reached the screen center, we flashed the detection line, resulting in the same physical and retinal stimulation as that in fixation trials. The bull's eye continued to move for another 500 ms. At the end of the trial, subjects had to indicate the position of the line. All conditions were presented interleaved.

EYE MOVEMENT ANALYSIS. We analyzed the eye movements in a 200-ms interval centered on the stimulus presentation. In this interval we calculated the average eye velocity. Trials in which a saccade occurred in this interval were excluded from further analysis (19%). Moreover, we excluded trials in which the pursuit gain (eye velocity divided by target velocity) was <0.7 (<1%).

RESULTS

Experiment 1

In *experiment* 1, we investigated how chromatic contrast sensitivity is influenced by OKN compared with fixation. OKN is of special interest because it is believed that the slow-phase component of at least look-nystagmus might be very similar to SPEM. To measure the influence of OKN on chromatic sensitivity, we presented a moving random-dot pattern and asked subjects to detect horizontal, colored lines.

First we describe the recorded eye movements (Figs. 1 and 2). The average horizontal amplitude of the fast phase amounted to 8.07° (SD 8.11°). In the vertical direction the average amplitude of the fast phase amounted to 0.24° (SD 0.64°). The duration of the slow phase was on average 0.67 s (SD 0. 35 s) and ranged between 0.2 and 2 s. The random-dot pattern took about 2.1 s to travel across the whole screen, which explains

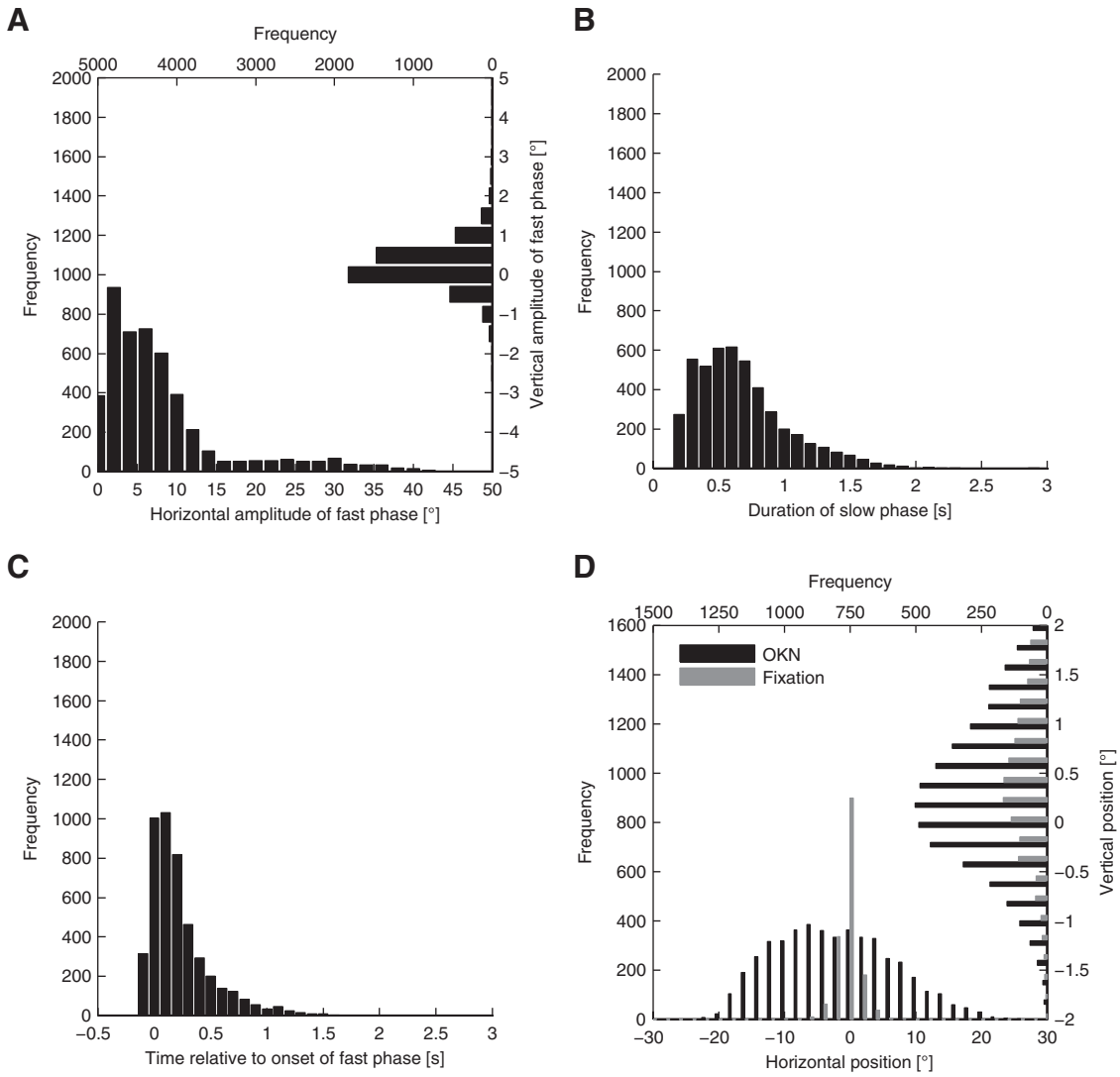

FIG. 2. *Experiment* 1: eye movement data for OKN. *A*: histograms of horizontal and vertical fast-phase amplitudes. *B*: histogram of slow-phase durations. *C*: histogram of stimulus onset times relative to fast-phase onsets. *D*: histograms of horizontal and vertical eye position at stimulus onset. Black indicates OKN, gray indicates fixation.

the upper limit of 2 s of the slow-phase duration. For stare-nystagmus the typical slow-phase duration is about 0.3 s (Carpenter 1988) and thus we obtained a mixture of stare- and look-nystagmus (Ter Braak 1936). Because there was no fixation point in the display, neither in OKN nor in fixation trials, the eye position at the time of stimulus presentation was scattered both during fixation and during OKN. We gathered psychophysical data from stimulus onset to fast-phase latencies of −0.1 to 1.5 s, but the frequency decayed rapidly with increasing delay to the fast-phase onset and therefore we restricted the psychophysical analysis to the interval of −0.1 to 0.5 s after fast-phase onset.

The psychophysical results show that the detection rate for the chromatic line stimuli increased after fast-phase onset (Fig. 3). In a similar way, response latencies for chromatic stimuli decreased after fast-phase onset. We correlated the detection rate and response latency for each subject and found for five of six subjects a significant negative correlation with a correlation coefficient below −0.7 (all P values <0.05). This shows that detection rate and response latency followed a similar, inverted pattern.

Based on the time average of the chromatic detection rate and the response latency, we decided to split the data into three intervals of 200 ms (Fig. 4). The first interval ranged from −0.1 to 0.1 s and covers the fast-phase OKN. The second interval ranged from 0.1 to 0.3 s and represents an early slow-phase OKN. The last interval ranged from 0.3 to 0.5 s and represents a late slow-phase OKN. We calculated for each

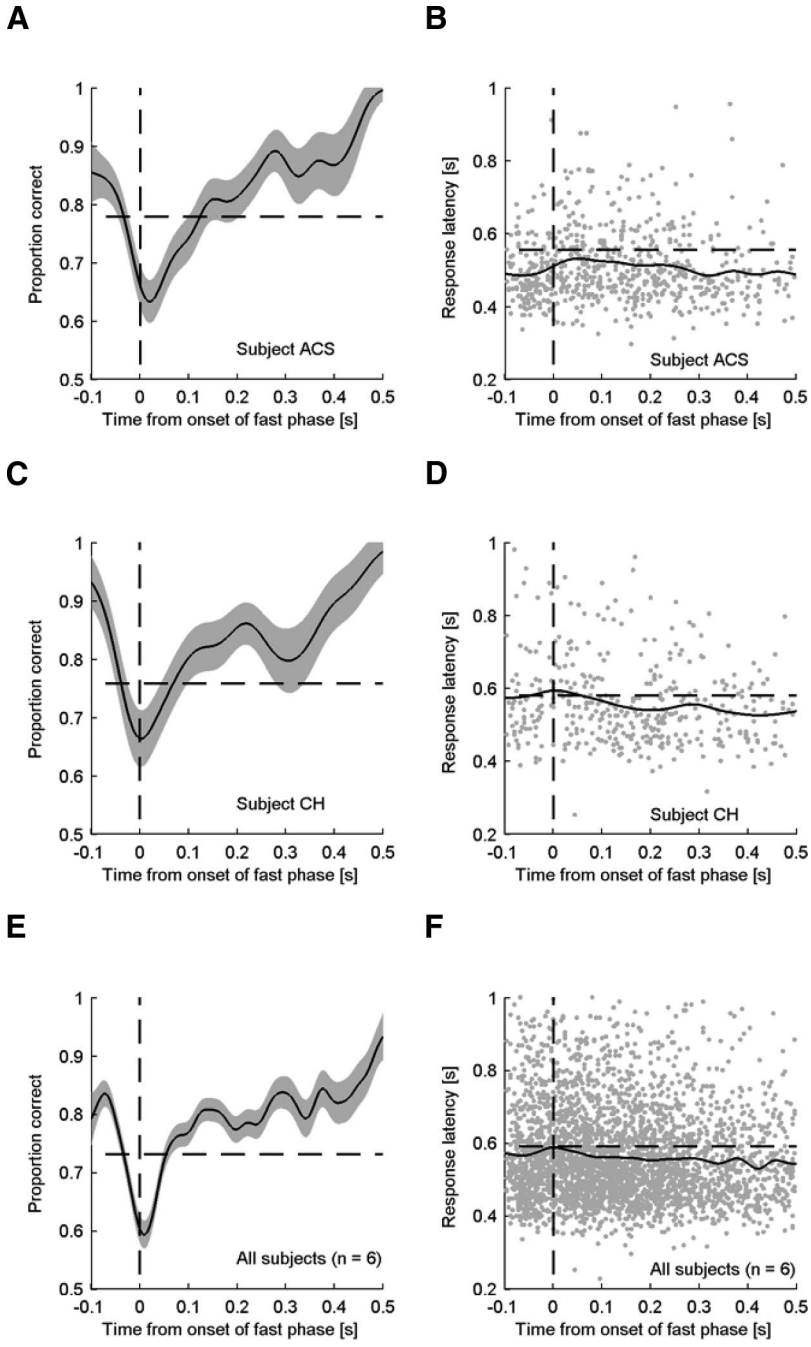

FIG. 3. *Experiment* 1: chromatic detection. Time course of detection rate (*A*, *C*, *E*) and response latency (*B*, *D*, *F*) relative to the onset of the fast phase of OKN. The black line indicates the average detection rate or response latency and the gray shaded area the respective SE. Gray dots indicate response latencies in individual trials. The horizontal dashed black line indicates detection-rate-respective response latency during fixation. The vertical dashed black line indicates fast phase onset. *A*, *C*, *E*: average detection rate. *B*, *D*, *F*: average response latency. *A* and *B*: data for subject ACS. *C* and *D*: data for subject CH. *E* and *F*: data accumulated over all subjects.

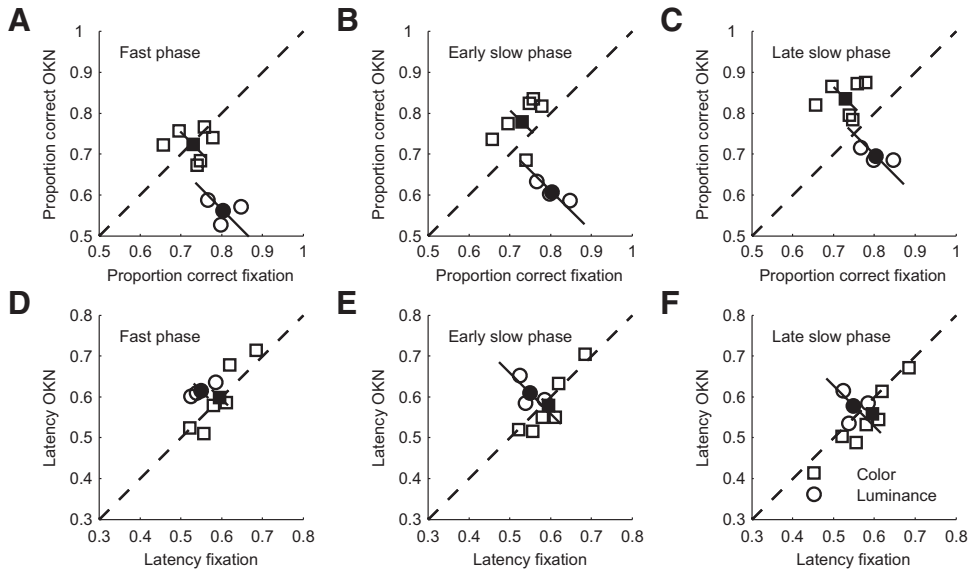

FIG. 4. *Experiment* 1: average detection rate and average response latency during different phases of OKN and fixation. *A–C*: average detection rate. *D–E*: average response latency. *A* and *D*: fast phase of OKN. *B* and *E*: early slow phase of OKN. *C* and *F*: late slow phase of OKN. Squares indicate data for chromatic stimuli; circles indicate data for luminance stimuli. The open symbols indicate individual data; the filled symbols indicate the mean over all observers. The diagonal error bars indicate the 95% confidence interval (CI) of the mean difference between fixation and OKN.

interval a *t*-test to check whether the detection rate and the response latency differed between OKN and fixation. In the fast-phase interval there was neither a significant difference for detection rate [$t(5) = 0.23$, $P = 0.831$] nor for response latency [$t(5) = 0.21$, $P = 0.845$]. In the early slow-phase interval, the detection rate increased by 6.8%, from 73% during fixation to 78% during OKN [$t(5) = 2.29$, $P = 0.071$] and the response latency decreased by 2.8%, from 595 ms during fixation to 578 ms during OKN [$t(5) = 1.27$, $P = 0.258$], although both differences were not significant. In the late slow-phase interval, the detection rate increased by 14.5% relative to fixation to a value of 83% during OKN [$t(5) = 4.76$, $P = 0.005$]. The response latency decreased by 6.1% to a value of 558 ms during OKN [$t(5) = 3.21$, $P = 0.024$]. Previously we found an increase of chromatic sensitivity during SPEM of 16% (Schütz et al. 2008). Unfortunately, we cannot directly compare the increase in detection rate with the previously measured increase of sensitivity. To obtain a rough comparison, we calculated how much the average psychometric function from the previous experiments had to be shifted along the contrast axis to obtain an increase of detection rate from 73 to 83%. According to our estimations a 14.5% increase of detection rate would correspond roughly to a 10.6% increase of sensitivity, based on the previously measured psychometric function.

As can be seen from Fig. 3, there was a transient reduction of detection rate for chromatic stimuli during the fast phase of OKN. Such a reduction of sensitivity might be caused by retinal slip of the horizontal line, induced by any vertical component of the fast phase. If this would be the case, detection rate and vertical fast-phase amplitude should be negatively correlated. To test this hypothesis, we selected all trials in which the line was presented within an interval of 50 ms centered on fast-phase onset. Next we binned these trials into six bins ranging from 0 to 1° vertical amplitude. For each bin the detection rate was calculated and arcsine transformed. A repeated-measures ANOVA showed no significant influence of the vertical fast phase amplitude [$F(5,20) = 0.870$, $P = 0.470$].

We performed a control experiment with three subjects to test luminance detection during OKN. During the fast-phase interval, the detection rate for luminance was 30.1% lower during OKN [$t(2) = 7.01$, $P = 0.017$]. The response latency during OKN was 12.0% longer in the fast-phase interval [$t(2) = 7.88$, $P = 0.016$]. In the early slow-phase interval, the detection rate was still significantly lower by 24.5% [$t(2) = 5.63$, $P = 0.033$], but the response latency tended to be only 11.1% longer [$t(2) = 1.73$, $P = 0.226$]. In the late slow phase the detection rate tended to be 13.4% lower during OKN [$t(2) = 3.36$, $P = 0.078$] and the response latency tended to be 5.3% longer [$t(2) = 0.93$, $P = 0.450$], although both differences were not significant.

Experiment 2

In *experiment* 2, we measured how chromatic and luminance sensitivity is affected during the visually enhanced VOR (VVOR). We asked subjects to rotate their head while keeping fixation at a stationary spot. During the active head movement, we presented chromatic and achromatic lines. In this paradigm, similar to SPEM, the eyes move smoothly, but the source of the movement is not a motion signal of a physically moving target. Instead, vestibular signals related to the head rotation are complemented by fixation and possibly by OKN mechanisms, but not by SPEM (Leigh et al. 1987). It has been shown that the gain is almost perfect for low frequencies ≤1.5 Hz (Atkin and Bender 1968; Medendorp et al. 2000; Takahashi et al. 1980).

If not stated otherwise, the methods are the same as those in *experiment* 1.

As expected the average eye-in-head velocity was somewhat larger than the average eye velocity in the OKN experiment (Fig. 5). On average, the eye-in-head velocity at the time of stimulus presentation was 27.66°/s (SD 6.19°/s). The average VVOR frequency amounted to 0.32 Hz (SD 0.05 Hz).

Figure 6 shows the sensitivity values for chromatic and achromatic stimuli, obtained during VVOR and during fixation. The sensitivity for chromatic stimuli was on average 13.4% lower during VVOR than that during fixation [$t(5) = 5.13$, $P = 0.004$]. For luminance stimuli, there was no significant difference [$t(5) = 0.75$, $P = 0.416$], although the average sensitivity was 6.6% lower during VVOR. We also compared sensitivities for luminance and color separately during fixation and VVOR. During fixation, sensitivity for luminance was 6.6%

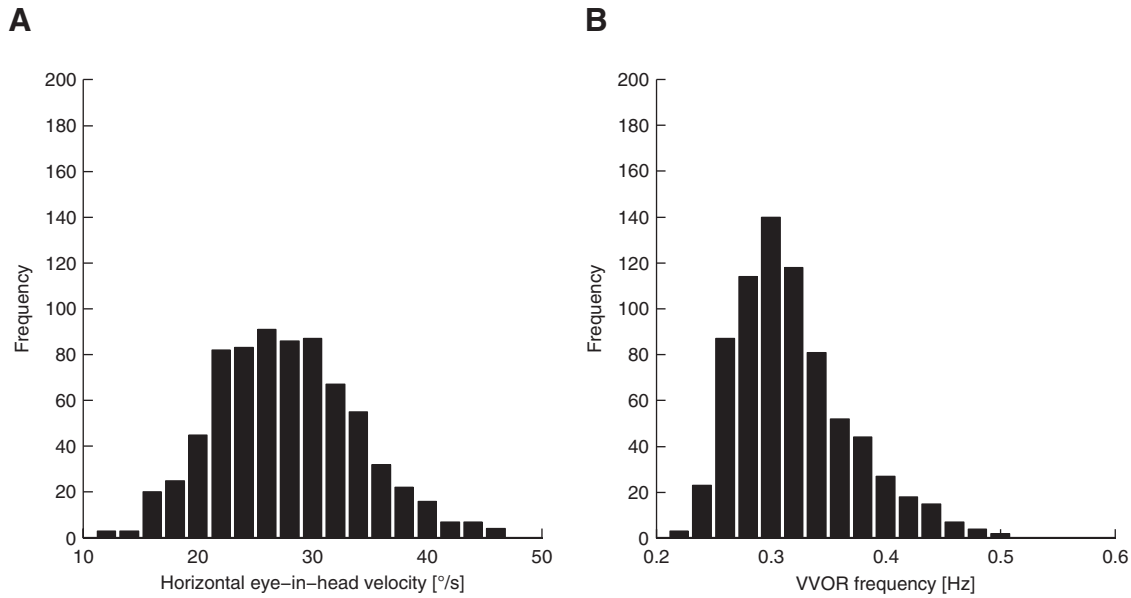

FIG. 5. *Experiment* 2: eye movement data for visually enhanced vestibulo-ocular reflex (VVOR). *A*: histogram of horizontal eye-in-head velocity at the time of stimulus presentation. *B*: histogram of VVOR frequency.

lower than sensitivity for color, but this difference was not significant [$t(5) = 0.75$, $P = 0.490$]. During VVOR, sensitivity for luminance was 2.4% higher than sensitivity for color. This difference was also not significant [$t(5) = 0.20$, $P = 0.850$].

Experiment 3

In *experiment* 3, we compared chromatic and luminance contrast sensitivity during fixation and during two pursuit conditions of different velocities. We tried to elicit SPEM with eye velocities similar to those measured during OKN (*experiment* 1) and VVOR (*experiment* 2).

We measured chromatic and luminance contrast sensitivity during horizontal pursuit with targets moving at 14.1 and 24.7°/s, to check whether the enhancement of chromatic sensitivity is also present at the observed eye velocities measured during VVOR. Figure 7 shows the color and luminance sensitivities normalized by the sensitivity obtained during fixation for the two velocities measured in this experiment and for the previously measured velocities (Schütz et al. 2008).

A two-way repeated-measures ANOVA (target velocity × stimulus condition) revealed a significant main effect of target velocity [$F(2,10) = 5.19$, $P = 0.028$] and a significant main effect of stimulus condition [$F(1,5) = 51.05$, $P < 0.001$]. The interaction between target velocity and stimulus condition was also significant [$F(2,10) = 26.51$, $P < 0.001$]. Thus SPEM influenced chromatic sensitivity and luminance sensitivity in a different way. Chromatic sensitivity was 33.5% higher during 14.1°/s pursuit than that during fixation [$t(5) = 5.40$, $P =$

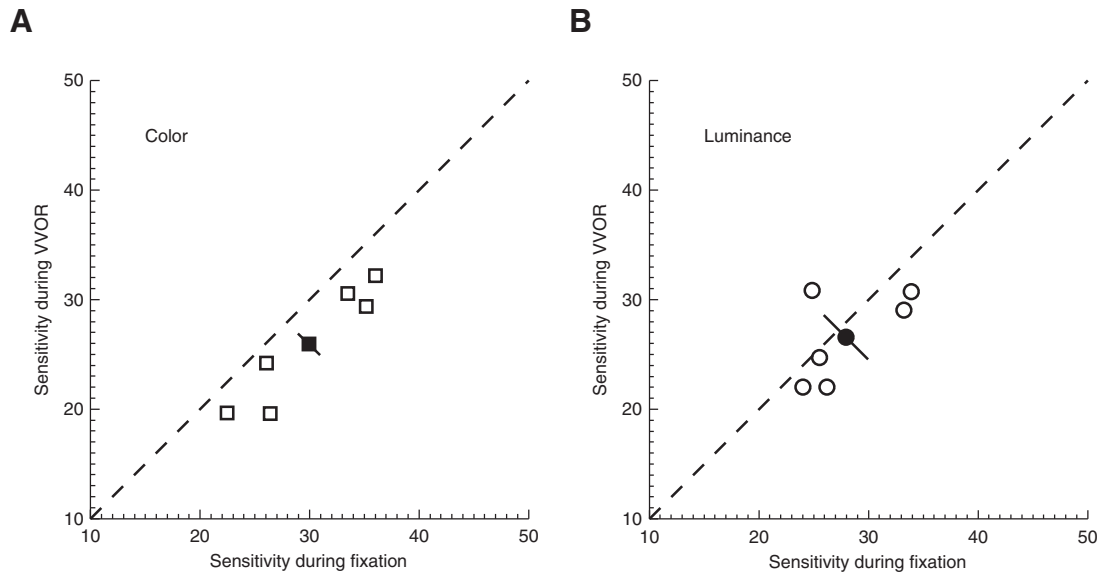

FIG. 6. *Experiment* 2: contrast sensitivity during VVOR. *A*: contrast sensitivity for chromatic stimuli. *B*: contrast sensitivity for achromatic stimuli. The open symbols indicate individual data; the filled symbols indicate the mean over all observers. The diagonal error bars indicate the 95% CI of the mean difference between the sensitivities during fixation and VVOR.

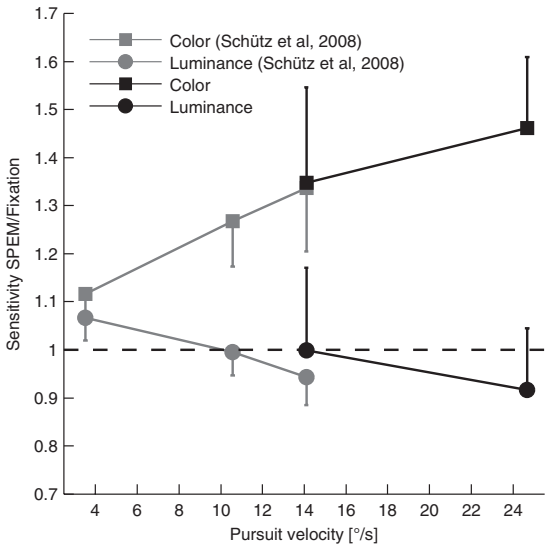

FIG. 7. *Experiment* 3: contrast sensitivity during smooth pursuit eye movement (SPEM). Relative sensitivity values compared with the sensitivities during fixation are shown. Circles represent achromatic stimuli; squares represent chromatic stimuli. The error bars represent the 95% CIs. The horizontal dashed line represents the sensitivity during fixation. The data plotted in gray is from Schütz et al. (2008); the data plotted in black was collected in the present study.

0.003]. This closely matches the previously measured threshold reduction of 24%, which is equal to a sensitivity improvement of 33% (Schütz et al. 2008). For 24.7°/s pursuit, chromatic sensitivity was increased by 47.1% compared with fixation [$t(5) = 5.83$, $P = 0.002$]. There is no significant difference between the sensitivities in the two pursuit conditions [$t(5) = 1.92$, $P = 0.114$], suggesting at least a saturation of the improvement above 14°/s. For luminance sensitivity, the picture is quite different. We did not observe any difference between fixation and 14.1°/s pursuit [$t(5) = 0.19$, $P = 0.854$]. For the faster pursuit condition, luminance sensitivity was on average 8.8% lower, but this trend was not significant [$t(5) = 1.62$, $P = 0.166$].

DISCUSSION

Experiment 1

The results showed an increase of chromatic detection rate during the slow phase of OKN. This increase significantly exceeded the fixation level in the late slow phase. However, even in the early slow phase, right after the fast phase, the detection rate tended to be higher than that during fixation. Moreover we observed a slight dip in the detection rate for chromatic stimuli during the fast phase of OKN. We showed that this transient reduction was not caused by retinal slip of the horizontal lines, which is induced by any vertical component of the fast phases. There are two other mechanisms that might result in a suppression of sensitivity. First, it might be that during the fast phases of OKN an effect similar to saccadic suppression occurs. However, saccadic suppression is known to affect only luminance stimuli with low spatial frequencies, but not stimuli defined by color (Burr et al. 1994). Second, it might be that the rapid movement of the structured background (i.e., the random-dot pattern) during the fast phases leads to retinal masking. For saccades it has been shown that visual masking strongly reduces contrast sensitivity (Campbell and Wurtz 1972; Diamond et al. 2000). Because the retinal image motion is very similar during fast-phase OKN and saccades, probably the same masking effects take place. For the response latency we found a decrease during the slow phase of OKN, which fell under the level of fixation at least in the late period of slow phase. We could also show that the course of the detection rate and the response latency were highly negatively correlated. This fits very nicely with previous studies showing decreasing reaction time (Harwerth and Levi 1978; Lupp et al. 1976; Tartaglione et al. 1975) and decreasing latency of visual evoked potentials (Mihaylova et al. 1999) with increasing contrast. At the same time we observed a reduced detection rate and a trend for an increased response latency for luminance stimuli during the slow phase of OKN. Taken together, both the increase in detection rate and the decrease in response latency indicate that chromatic sensitivity is enhanced during the slow phase of OKN. Because we did not measure contrast sensitivity, we cannot directly compare the magnitude of enhancement during slow-phase OKN and during SPEM. Nonetheless, we think that it is quite plausible that both phenomena are tightly related.

Besides our results for contrast detection, similarities in the perceptual consequences of SPEM and OKN have also been observed for localization performance. The pattern of spatial mislocalization is similar during slow-phase OKN (Kaminiarz et al. 2007, 2008; Tozzi et al. 2007) and during SPEM (Brenner et al. 2001; Kerzel et al. 2006).

Classically, SPEM and OKN have been considered as distinct types of eye movements (Carpenter 1988) and there are indeed some differences between SPEM and OKN. For instance, it has been shown that SPEM can be performed to second-order motion (Butzer et al. 1997; Hawken and Gegenfurtner 2001; Lindner and Ilg 2000), whereas OKN is not elicited by second-order motion alone (Harris and Smith 1992), although consistent second-order motion can increase the OKN response to first-order motion (Harris and Smith 2000). Newer evidence, however, suggests that these eye movements are more closely related at the neural level. It has been shown that lesions of the nucleus of the optic tract and the dorsal terminal nucleus of the accessory optic system impair not only OKN, but also SPEM (Ilg et al. 1993). A functional magnetic resonance imaging study revealed a large overlap between the neural circuits for SPEM and OKN (Konen et al. 2005). Interestingly, look-nystagmus evoked similar activity in cortical oculomotor areas like SPEM, such as the frontal eye fields (FEFs) and the supplementary eye fields (SEFs), whereas stare-nystagmus failed to activate these areas. Thus it seems that neural differences arise not primarily between OKN and SPEM, but between stare- and look-nystagmus. Based on the definition (Ter Braak 1936) and the instruction to the subjects we observed a mixture of both stare- and look nystagmus in our study. Thus we cannot draw a reliable conclusion about stare-nystagmus, although at least we can state that an improved chromatic sensitivity is present during look-nystagmus because the improvement occurred especially at long slow-phase durations, which are specific for look-nystagmus.

Another dissociation between subtypes of OKN stems from results of patient studies. It is known that the gain of SPEM is reduced in patients suffering from schizophrenia (Holzman et al. 1973; Trillenberg et al. 2004), which is probably caused by a deficit in velocity processing (Chen et al. 1999). A compar-

ative study found a similar deficit for partial-field OKN, but not for full-field OKN (Latham et al. 1981). Because we presented our OKN stimulus on a computer screen, we definitely tested partial-field OKN. Possibly, partial-field OKN is more likely to induce look-nystagmus and full-field OKN is more likely to induce stare-nystagmus. Further evidence for a similarity of OKN and SPEM comes from developmental studies. Both types of eye movements evolve at the same age (Rosander and von Hofsten 2002) and their occurrence coincides with the maturation of motion direction sensitivity (von Hofsten 2004).

Experiment 2

In contrast to the results measured during SPEM (Schütz et al. 2008) and during OKN (*experiment* 1), we found no significant improvement of chromatic sensitivity during VVOR. Instead chromatic contrast sensitivity was lowered by 16% during VVOR. For luminance sensitivity, we did not find any significant difference between fixation and VVOR, although the average sensitivity tended to be 5% lower during VVOR.

Several other studies measured perceptual performance during VOR. All of these studies used luminance-defined targets to measure perceptual performances. Studies about reading performance (see Benson and Barnes 1978 for a review) during VOR did not find any perceptual deficits up to frequencies of 9 Hz. Another study measured contrast sensitivity for gratings in two viewing conditions (Flipse and Maas 1996): in the first condition passive head movements were applied, subjects performed VOR, and the residual retinal image motion was measured; in the second condition the head was kept fixed and the stimulus moved physically according to the measured retinal image motion. The results did not show any sensitivity differences between actual VOR and simulation of the residual retinal velocity occurring during VOR. A major difference from these studies is that we measured contrast sensitivity during active head rotation. Unfortunately, we do not have the experimental equipment at hand at this time to properly test passive VOR. Regarding the quality of image stabilization, active head rotation is either similar (Takahashi et al. 1983) or slightly better than passive rotation (Collewijn et al. 1983). As we pointed out earlier, active and passive head rotations also cause differential neural activity (Cullen and Roy 2004; Roy and Cullen 1998, 2002). More recently it has been shown that the amount of perceived motion smear is reduced during VOR (Bedell and Patel 2005) and during the inhibition of VOR (Tong et al. 2005). Both studies also used passive head rotation. Because the reduction of motion smear also occurs during passive movements of the eyes, it is at least partially driven by proprioceptive feedback of the eye muscles (Tong et al. 2008). The dissociation we found between the changes of perceived motion smear and the enhancement of chromatic sensitivity leaves two different interpretations: *1*) either the observed changes of motion smear and chromatic sensitivity are not related to each other or *2*) there is a qualitative difference between active head rotation and passive head rotation.

There are several reasons that might explain the decrease of chromatic sensitivity during VVOR. First, it might be that the decrease in sensitivity is caused by the attentional demands of the head movement. The fact that we found a trend for a suppression of chromatic as well as luminance sensitivity suggests a general decline of visual performance during VVOR. In that view, the active head movement would represent a second task, which might draw attention from the perceptual task. As a further requirement, fixation had to be kept at the fixation target, which was also not required during OKN. A second reason might be that there was some residual retinal image motion due to imperfect VVOR. Although we cannot refute this possibility with our data, it seems to be rather implausible. Our stimulus was aligned horizontally, so that horizontal retinal image motion should not influence the perceptual performance. Strong vertical eye movements, however, are quite unexpected during horizontal VVOR, so that no substantial retinal image motion should occur. The third explanation relates to the measured eye velocities. During SPEM, we measured a chromatic improvement up to a pursuit velocity of 14.1°/s. For that velocity range, chromatic sensitivity increased with increasing pursuit velocity. However, the average eye-in-head velocity during VVOR was on average twice as large, which could be the reason that we did not observe any improvement of chromatic sensitivity in this experiment. In general it is desirable to keep conditions as similar as possible. Unfortunately, our subjects were not able to maintain consistent head movements at lower head velocities. Thus we were not able to measure active VOR with lower head velocities. Surely chromatic sensitivity will not rise to infinity for fast pursuit velocities and it even might be that the improvement decays for higher velocities. To test this possibility we performed a third experiment, in which we measured contrast sensitivity during pursuit of higher velocities.

Considering the neural basis of SPEM and VVOR, it is not very surprising that we found different effects on chromatic sensitivity. The basic pathway for VOR is a trisynaptic connection between primary and secondary vestibular neurons and oculomotor neurons (Lorente De Nó 1933). Classically, this connection has been viewed as a hard-wired reflex. However, now it is known that the activity of neurons in the vestibular nuclei is modulated by the current gaze strategy (Cullen and Roy 2004; Roy and Cullen 1998, 2002). This is especially important during combined eye and head gaze shifts. Furthermore, the cerebellum is required for the adaptive modification of the VOR (du Lac et al. 1995; Lisberger 1988; Raymond et al. 1996). The pure vestibular VOR can be studied only in complete darkness. In an illuminated environment, as in our experiment, VOR is always supplemented by fixation, but not by SPEM (Leigh et al. 1987). Moreover, in the frequency range of our experiment, of around 0.2 to 0.5 Hz, VOR and OKN act synergistically to stabilize gaze. For lower frequencies, however, gaze stabilization is mainly driven by OKN, whereas VOR dominates gaze stabilization for higher frequencies (Schweigart et al. 1997). We found an increase of chromatic sensitivity during OKN but not during VVOR. Possibly, the active fixation mechanism during VVOR prevents enhanced chromatic sensitivity.

SPEM, in contrast, is controlled by a cerebro-ponto-cerebellar network (see Krauzlis 2004, 2005; Thier and Ilg 2005 for reviews). Important cortical structures are the middle temporal area (MT), the medial superior-temporal area (MST), the SEFs, and the FEFs. In the brain stem, the pontine nuclei and the nucleus reticularis tegmenti pontis are involved in SPEM. In the cerebellum, two areas are involved in the generation of SPEM: the flocculus–parafloccculus complex and the posterior

vermis. Thus the neural circuits for SPEM and VOR do not overlap. Interestingly, it has been shown that VOR matures earlier than VOR inhibition and SPEM (Finocchio et al. 1991; Rosander and von Hofsten 2000), which provides further evidence that SPEM and VOR are distinct types of eye movements.

Based on psychophysical results (Schütz et al. 2008), we previously argued that the signal that triggers the enhancement has to match two criteria: it has to precede the onset of SPEM and it has to be related to pursuit velocity. We also speculated that at least two areas match these criteria: the FEF and area MST. FEF neurons are involved in pursuit gain control (Churchland and Lisberger 2002; Schwartz and Lisberger 1994; Tanaka and Lisberger 2001). MST neurons encode target motion in world-coordinates (Ilg et al. 2004) and show activation during anticipatory pursuit (Ilg 2003), as well as during pursuit of an imaginary target (Ilg and Thier 2003). Both areas have been shown to be active during SPEM as well as during look OKN (Konen et al. 2005), which fits nicely with our finding of *experiment* 1 that chromatic sensitivity was enhanced during both SPEM and OKN. Furthermore, it has been shown that the so-called visual tracking neurons in MST are active during SPEM and VOR inhibition, but not during VOR (Freeman 2007; Ono and Mustari 2006), which is consistent with our finding that chromatic sensitivity was enhanced during SPEM but not during VVOR.

Experiment 3

To summarize, this experiment extends the previously reported enhancement of chromatic sensitivity to pursuit velocities $\leq$24°/s: the improvement increased steadily with pursuit velocity $\leq$14°/s and saturated above. This shows that the absence of a chromatic improvement during VVOR (*experiment* 2) is not due to the larger eye velocity.

For luminance sensitivity we did not find any signs for an improvement, but a nonsignificant trend for a reduction of sensitivity with increasing pursuit velocity. This is in line with a significant suppression of peripheral sensitivity for low-spatial frequency luminance stimuli in previous experiments (Schütz et al. 2007b, 2008). In the present study we did not focus on this smaller effect and therefore had not enough statistical power in *experiment* 3.

Conclusion

In our comparative study we investigated whether the recently found enhancement of chromatic sensitivity during SPEM (Schütz et al. 2008) is a more general property of slow eye movements. Slow continuous eye movements help to prevent image slips on the retina that occur whenever we move our head, eyes, or the whole body. Primates can actively follow moving objects with their eyes and they can also keep their eyes on stationary objects when they move their head. Slow eye movements also occur during the slow phase of the optokinetic response to retinal image motion during head movements.

In a series of experiments we studied whether OKN and VVOR exhibit the same influence as that of SPEM on chromatic contrast sensitivity, given that the eye velocity is similar in all conditions. We obtained an increased chromatic sensitivity during the slow phase of OKN and a decreased sensitivity during VVOR. Because the eye-in-head motion was substantially faster in the VVOR experiment, we also tested chromatic sensitivity during fast SPEM. This control experiment showed an enhanced chromatic sensitivity even for high pursuit velocities, similar to those measured during VVOR, ruling out the explanation that eye velocities were too high in the VVOR experiment.

Beside the differential effects on chromatic sensitivity we report here, there is another important distinction between OKN and SPEM on the one hand and VVOR on the other hand. During both OKN and SPEM there is a physically moving stimulus present, which is not true for VVOR. This dissociation is also reflected in the activity of tracking neurons in area MST (Freeman 2007; Ono and Mustari 2006). These neurons show activity during active tracking of a moving stimulus, irrespective of whether the stimulus is tracked by eye or head movements. However, these neurons are silent during both VOR and VVOR, although the eye-in-head motion is more similar between SPEM and VVOR. Since the perceptual enhancement of chromatic stimuli is an active process, neurons in area MST could play a critical role in the generation of the top-down signals that change sensitivity in earlier visual areas.

ACKNOWLEDGMENTS

We thank T. Freeman, L. Harris, and two anonymous reviewers for helpful discussion; E. Baumgartner for help with data collection; and our subjects for participation.

GRANTS

This work was supported by Deutsche Forschungsgemeinschaft (DFG) Forschergruppe FOR 560 "Perception and Action" and DFG Graduiertenkolleg GRK 885 "NeuroAct."

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