

Brief communication

Suppression of optokinesis during smooth pursuit eye movements revisited: The role of extra-retinal information

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Abstract

When our eyes track objects that are moving in a richly structured environment, the retinal image of the stationary visual scene inevitably moves over the retina in a direction opposite to the eye movement. Such self-motion-induced global retinal slip usually provides an ideal stimulus for the optokinetic reflex. This reflex operates to compensate for global image flow. However, during smooth pursuit eye movements it must be shut down so that the reflex does not counteract the voluntary pursuit of moving targets. Here, we asked if retinal information is sufficient for this cancellation of the optokinetic reflex during smooth pursuit eye movements. In a series of experiments, we show that neither the eye movement-induced retinal image motion per se nor the relative motion between the pursuit target and the background are sufficient for suppression of optokinesis. We, therefore, conclude that extra-retinal information about smooth pursuit eye movements is required for the cancellation of the optokinetic reflex.

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1. Introduction

One of the big challenges for most animal species and humans is to provide their visual system a stable retinal image of the world despite self-motion. This is usually accomplished by gaze-stabilizing reflexes such as the optokinetic reflex (OKR). However, during smooth pursuit of moving targets this reflex has to be suppressed as it would otherwise counteract the voluntary eye movement: while tracking a moving object of interest, the image of the stationary world will inevitably slip over the retina in the opposite direction. Such global image motion reflects an ideal stimulus for the OKR which consequently would try to move the eyes in a direction opposite to the pursued target. Thus, the OKR must be switched off during such smooth pursuit eye movements (SPEM). Otherwise, voluntary pursuit would become impossible.

Suppression of optokinesis is already reflected by our ability to pursue moving objects in front of a stationary, textured background. In fact, previous studies report only slight reductions of eye velocity (5–10%) during the maintenance of SPEM in the presence of an optokinetic background as compared to pursuit of a single target in an otherwise dark environment (man: Collewijn & Tamminga, 1984; Yee, Daniels, Jones, Baloh, & Honrubia, 1983; monkey: Ilg, Bremmer, & Hoffmann, 1993; Ilg & Hoffmann, 1996; Mohrmann & Thier, 1995). Other studies even failed to detect these minor influences of optokinetic backgrounds on pursuit (Keller & Khan, 1986).

Large OKR-induced modulations in SPEM velocity can be observed if shifting a structured background suddenly and in any direction apart from the direction of pursuit-induced global image flow (Kodaka, Miura, Suehiro, Takemura, & Kawano, 2004; Lindner, Schwarz, & Ilg, 2001; Schwarz & Ilg, 1999; Suehiro et al., 1999). This finding demonstrates a direction-specificity of OKR suppression. Furthermore, it directly reflects the necessity to cancel

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the OKR due to SPEM-induced motion while guaranteeing the ability to counteract any other kind of unexpected global image motion. Yet, the question of how the oculomotor control system manages to switch off the OKR during SPEM in such an ecologically plausible manner has still to be answered. At present, there is only preliminary experimental evidence implying that either the relative motion between the pursuit target and the background, or, alternatively, the pursuit-induced background image motion per se might be used as purely visual cues to suppress the OKR in the direction of self-produced image motion (Kodaka et al., 2004; Suehiro et al., 1999; Wyatt & Pola, 1984). We, therefore, tried to test thoroughly whether such visual information is sufficient for the direction-specific cancellation of the OKR during SPEM or whether extra-retinal information like for instance an efference copy (von Holst & Mittelstaedt, 1950) or corollary discharge (Sperry, 1950) of the voluntary eye movement motor command might be additionally needed.

2. Methods

2.1. Experimental paradigms

Our experimental approach was to use global motion-induced modulation of eye velocity as an experimental probe to determine whether specific kinds of visual information are sufficient for suppressing the OKR during SPEM. SPEM were guided by a red target dot ($0.3^\circ \times 0.3^\circ$; 9.5 cd/m^2), which randomly stepped 2° to the left or to the right after a variable period of fixation before it started to move with a constant velocity of $10^\circ/\text{s}$ in direction opposite to the step for 1000 ms. This ‘step-ramp’ paradigm (compare Rashbass, 1961) was engaged to avoid an initial saccade to the pursuit target. This was important because such saccades might have obscured the global motion-induced modulation of eye velocity. Throughout the entire step-ramp trial, a structured background pattern was visible. The pattern consisted of 400 vertical, white line elements ($\sim 0.1^\circ \times 0.3^\circ$; 35 cd/m^2) on an otherwise dark ($0,0 \text{ cd/m}^2$) background which subtended $45^\circ \times 41^\circ$. In our control condition, this background remained stationary throughout the trial, whereas, in all other trials the background unexpectedly shifted either in the direction of pursuit or in the opposite direction. Such shifts always lasted for 200 ms. Within this period the background was moving “*en bloque*” at a constant velocity of $20^\circ/\text{s}$. According to our previous findings (Lindner et al., 2001; Schwarz & Ilg, 1999) an OKR-induced modulation of SPEM velocity was to be expected whenever the background shifted in direction of target motion (in-phase). However, background motion in the opposite direction (counter-phase) should not elicit any modulation because of OKR suppression in direction of self-induced image flow. All visual stimuli were presented on a CRT monitor (frame rate 60 Hz) in a dark experimental room.

In the first experiment (‘background motion onset experiment’) we tested whether this direction-specific cancellation of the OKR also occurs in situations where the structured background starts to move before SPEM has actually been initiated, i.e., no SPEM-induced image motion is available prior to the background shift. To this end, we varied the starting time of the background shift relative to pursuit target onset. Stimulus onset asynchronies (SOAs) were chosen 0, 100, and 200 ms, respectively. All conditions were presented randomly interleaved and with an equal share of 2/7 (1/7 in-phase and 1/7 counter-phase background shifts). The remaining pursuit trials (1/7) consisted of the control condition, engaging SPEM over a stationary structured background. Sixty trials (30 trials leftward and 30 trials rightward SPEM) were registered for each condition and for each subject.

In a second experiment (‘blink experiment’) we asked whether the relative motion between the pursuit target and the background is necessary to suppress the OKR during SPEM. Similar to the *background motion onset experiment*, brief pulses of background motion were applied in a subset of trials while the SOA of the background shift was always set to 200 ms. The critical parameter in this experiment was the presence (relative motion) or absence (no relative motion) of the pursuit target around the time of the background shift: in randomly selected trials the pursuit target disappeared 150 ms after target movement onset. The target kept on moving invisibly for 300 ms until it reappeared for a further 550 ms. In other words, the pursuit target disappeared 50 ms before background motion onset and reappeared 50 ms after its offset. SPEM trials with (50% share) and without (50% share) target extinction were presented randomly interleaved. Trials engaging pursuit across a stationary structured background served as a control condition. Again, 60 trials were registered for each possible stimulus combination and for each of our subject.

Finally subjects conducted a ‘fixation experiment’ which tested for optokinetic responses during stationary fixation. The experiment resembled the timing and the principle design of the *blink experiment* with the only difference being that the fixation target remained stationary throughout the entire trial. The fixation spot vanished for 300 ms in half of trials. In the remaining half of trials the target remained visible throughout the trial. The background remained stationary in one-third of the trials. It unexpectedly moved to the right for 200 ms in one-third of trials and it shifted leftward in one-third of trials. Sixty trials were registered for each subject and each experimental condition. All conditions were presented in a randomly interleaved fashion.

2.2. Subjects

Six subjects, including the investigators (A.L. and U.J.I.), participated in the experiments. All of them had normal or corrected to normal visual acuity. Subjects gave their written informed consent according to the declaration of Helsinki.

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