

Coordination of smooth pursuit and saccades

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Abstract

Smooth pursuit and saccades are two components of tracking eye movements. Their coordination has usually been studied by investigating latencies of pursuit onset in response to a moving target appearing simultaneously with the disappearance of the stationary fixation target. The general finding from such studies has been that latencies of saccades and pursuit are different and reflect independent processes. We discuss several limitations of the used targets. In this paper, we study latencies of saccades and smooth pursuit in response to a moving target that overlaps in time with a pursued moving target. We find that saccades and pursuit changes are synchronized. Furthermore, pursuit changes are made fast. Directional changes occur almost entirely within the accompanying saccade. To explain the results we hypothesize a two-stage mechanism for the coordinated generation of saccades and pursuit.

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1. Introduction

Tracking eye movements consist of two different components, namely, smooth pursuit and saccades. Smooth pursuit, or just pursuit, is a class of rather slow eye movements that minimizes retinal target motion. Saccades are rapid eye movements that align the fovea with the target. Much is known about the behavior of pursuit and saccades (Kowler, 1990), the sensory regions of the brain that provide inputs for these movements and the motor pathways that execute them (pursuit: Lisberger, Morris, & Tychsen, 1987; saccades: Sparks & Mays, 1990).

The older neurophysiological literature emphasized differences between neuronal pathways for pursuit and saccades. Eye movement studies showed that dynamics of pursuit and saccades differed strongly and that latencies to motion onset were very different too (pursuit: 100–125 ms; saccades: 200–250 ms). Neurophysiological and behavioral differences together led to the conviction

that pursuit and saccades are controlled by predominantly independent neural mechanisms (see review in Leigh & Zee, 1991). However, more recent neurophysiological studies suggest that saccadic and smooth eye movement pathways are not independent in premotor structures like the superior colliculus (Krauzlis, Basso, & Wurtz, 2000; Missal, Lefevre, Delinte, & Crommelink, 1996; Olivier, Grantyn, Chat, & Berthoz, 1993) cerebellar vermis (Krauzlis & Miles, 1998; Suzuki & Keller, 1988) and mesencephalic reticular formation (Missal, de Brouwer, Lefevre, & Olivier, 2000). Furthermore, modulation of omnipause neurons during smooth pursuit suggested that the final pathways for saccades and smooth pursuit partially overlap or share an important group of neurons (Missal & Keller, 2002). These findings support the view that neural processes underlying pursuit and saccades are intertwined. In a very recent review, Krauzlis (2004) goes as far as proposing that pursuit and saccades are different outcomes from a single cascade of sensory-motor functions rather than results of two distinct neural systems.

Behavioral support for coordination of pursuit and saccades has been obtained from studies of pursuit

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onset. Evidence for coordination comes mainly from reports that pursuit and saccades share processing at the level of response preparation (Gardner & Lisberger, 2001, 2002; Liston & Krauzlis, 2003). There is also evidence that releases from fixation at the start of pursuit and saccades are mediated by mechanisms that have shared inputs (Krauzlis & Miles, 1996c). Shared neural circuits in target selection and in release from fixation appear not to result in synchronized onsets of saccades and pursuit. Kimmig, Biscaldi, Mutter, Doerr, and Fischer (2002) studied pursuit and saccadic latency in response to sudden target movement at constant velocity (motion ramp). Target motion was preceded by target displacement (target step), and occasionally preceded by a temporal gap in which the target disappeared from the screen. Step and ramp were chosen in the same direction to induce saccade and pursuit together. In step-ramp stimuli, pursuit started before a saccade in 46% of the trials. In gap-step-ramp stimuli, the percentage was 37%. A few other studies showed that latencies of pursuit were typically 25–75 ms shorter than those of saccades (Adler, Bala, & Krauzlis, 2002; Krauzlis & Miles, 1996a; Krauzlis, Zivotovsky, & Miles, 1999).

It is not certain that latencies of smooth pursuit and saccadic onsets are reliable indicators of independent pursuit and saccadic systems. A reason for doubt is that latencies have mainly been measured in response to onset of target motion after extinction of a stationary fixation point (Adler et al., 2002; Kimmig et al., 2002; Krauzlis & Miles, 1996a; Krauzlis et al., 1999). Several studies have indicated that fixation should not be viewed as pursuit of a stationary stimulus. Robinson (1965) showed that changes in visual feedback have little influence on eye position during fixation but produce large oscillations during pursuit of a moving target. High-frequency vibration imposed on a target does not affect fixation but produces large oscillations during pursuit (Goldreich, Krauzlis, & Lisberger, 1992). Similarly, discrete perturbations of a target produce smooth changes in eye speed during pursuit but not during fixation (Krauzlis & Miles, 1996b; Morris & Lisberger, 1987; Schwartz & Lisberger, 1994). A problem of motion onset latencies is that latencies of both pursuit and saccades are affected by the extinction of the fixation target per se, when it occurs at (step stimulus) or prior to (gap stimulus) the onset of target motion (Coubard, Daunys, & Kapoula, 2004; Fischer, 1987; Krauzlis & Miles, 1996a; Merrison & Carpenter, 1995; Saslow, 1967). Another argument of being cautious about results from step and gap stimuli is that these stimuli are very unusual in daily-life vision. The natural condition is that stimuli remain visible when other, already visible or newly appearing, stimuli are considered for pursuit. The present study was undertaken to measure latencies of sustained pursuit and saccadic in two paradigms, the traditional step paradigm and a paradigm in which

moving stimuli overlapped temporally. The results show that pursuit latencies were very different in the two paradigms. Furthermore, pursuit and saccadic latencies correlated poorly in the step condition and strongly in the overlap condition.

2. Methods

2.1. Subjects

Five human subjects, 25–53 years old, participated in two experiments. Experimental procedures were reviewed and approved by the Institutional Review Board and each subject gave informed consent. None of the subjects showed any visual or oculomotor pathology other than refraction anomaly. Subjects had normal or corrected-to-normal visual acuity. Four subjects were naïve with respect of the purpose of the experiment.

2.2. Eye-movement recording

We recorded movements of the left eye using an infrared video-based eye-tracker system (SR Research, EyeLink). The eye tracker reported the horizontal and vertical positions of the pupil with 12-bit resolution using an algorithm that computes the centroid of the pupil at 250 Hz. During the experimental sessions, subjects used a chin rest to minimize measurement errors due to head movements. The eye-tracker system measured and compensated for remaining head movements. Noise and accuracy of the eye position data was computed from measurements during which the subjects fixated the central fixation point ten times for periods of 1 s. Noise levels, computed as mean SDs (averaged over all subjects), were 0.05° for horizontal eye position and 0.08° for vertical eye position. At the start of each series of trials, the output from the eye tracker was calibrated by recording the eye positions as subjects fixated a set of nine fixation markers at known locations in a pseudorandom sequence.

2.3. Stimuli presentation, data collection and analysis

Stimuli were presented on a LaCie monitor (1280 × 1024 pixels, 75 Hz), positioned at a distance of 40 cm in front of the subject. The presentation of stimuli, timing of data recording, and storage of data were controlled by a Macintosh G4 computer running on OS 9. The EyeLink computer collected the eye position data that were transferred to the main computer via an Ethernet connection after each trial. All eye-movement data, and events related to the onset and offset of targets, were stored on disk during the experiment to be used for off-line analysis.

Analysis of pursuit concentrated on changes in pursuit direction (Fig. 1). Pursuit direction was obtained from the eye position data by computing the angles between eye positions that were 100 ms apart. To reduce

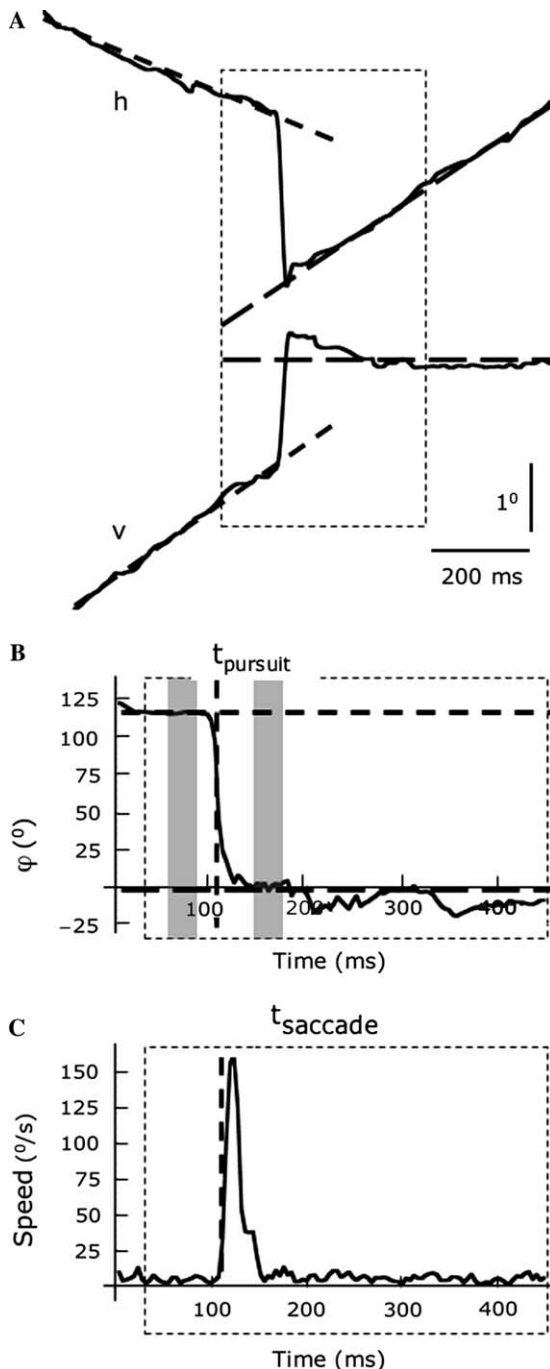


Fig. 1. (A) Horizontal (h) and vertical (v) eye position traces recorded in the T condition (dashed traces indicate the two temporally overlapping targets). The dashed rectangle indicates the time window for which the computed pursuit direction is shown in (B) and pursuit speed is shown in (C). Two grey bars in (B) indicate the time windows that were used for the computation of $\phi_{\text{pursuit_pre}}$ and $\phi_{\text{pursuit_post}}$. The rightward direction is defined as 0° with angles increasing in the counterclockwise direction.

noise to an acceptable level, a double-sided exponential filter with 8 ms time constant smoothed the computed direction signals. The onset of changes in pursuit direction (t_{pursuit}) was defined as the time at which pursuit direction first differed by 15° or more from the old target's directions and the difference remained above that level for a period of 200 ms (Fig. 1B). Visual inspection showed that this criterion was reliable except when the differences between the old and new target's directions were small. For that reason all responses to changes in target direction smaller than 30° were excluded from further analysis.

To identify saccades (Fig. 1C), velocity signals were computed from the horizontal and vertical eye position signals by applying a discrete four-point differentiation method, effectively filtering the data within a temporal window of 16 ms, centered about each data point (with exception of the first and last two data points of each trial). Saccades were detected by a threshold of 40 deg/s applied to the absolute speed signal, computed from the horizontal and vertical velocity signals. The time associated with saccade detection was designated as the time of saccade onset (t_{saccade}). Inspection of the eye position signals after removal of the detected saccades, showed that the method of saccade detection was reliable in detecting saccades larger than 0.3°.

2.4. Experimental paradigm

Two pursuit targets (crosses of 0.5°), one bright (18 cd/m²) and one dark (0.3 cd/m²), were presented alternately against a uniform grey background (7 cd/m²). Subjects were instructed to pursue the new target as soon as it appeared. The targets moved at constant velocity. Direction of motion, speed and presentation time were selected randomly: direction of motion over 360° with a resolution of 1°, speed between 4 and 12 deg/s, and presentation time between 1 and 3 s. Transitions between targets occurred in two ways. In one condition (N = no temporal overlap), the old target disappeared and the new target appeared simultaneously (Fig. 2, left side). In the other condition (T = temporal overlap), the two targets overlapped temporally (Fig. 2, right side), the old target remaining visible for 300–500 ms after the new target's appearance. Locations of appearance were chosen randomly within a radius of 5° from the location of the old target at the time of the new target's appearance. Directions of step and motion of the old and new targets were unrelated. Each condition was run in separate blocks of 4 trials of 15 s each, preceded by a calibration trial. All subjects completed 4 runs, comprising a total of 32 trials. On average 8 new targets appeared per trial, so that about 5 (subjects) \times 32 (trials) \times 8 (target changes) = 1280 pursuit changes were analyzed.

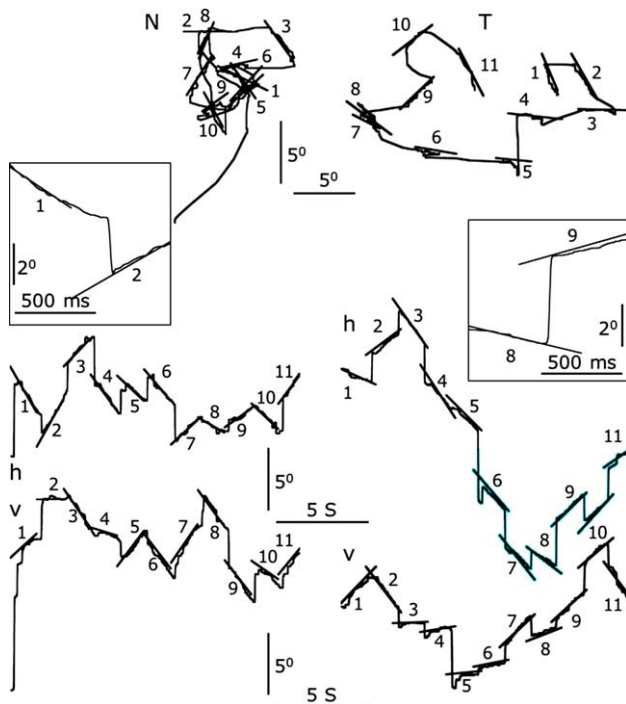


Fig. 2. Examples of eye movements in the N (left) and T (right) conditions. Eye and target movements are presented as x - t (h), y - t (v) and x - y (top) traces. Numbers indicate the sequential order of targets in the trials. The outlined magnifications illustrate typical behavior in the two conditions: pursuit changes occurring prior to the saccade (N); pursuit changes made within the saccade (T).

3. Results

The computed pursuit and saccade onsets were used to estimate Δt , the time period elapsed between t_{pursuit} (Fig. 1B) and t_{saccade} (Fig. 1C). Saccade detection was limited to 400 ms after the onset of new targets. Later saccades were deemed to have no relationship with the onset of new targets. As a consequence of this decision, changes in pursuit direction that could not be associated with saccades, were excluded from further analysis. Responses to first target's onset of each trial were also excluded from analysis, because these responses were regarded as switches from fixation to pursuit instead of as changes in sustained pursuit. We used Student's t -test to test for statistical significance. Eye movement analysis produced 96 valid data points on average with a minimum of 76 data points per subject and condition. All data were pooled over subjects because, with respect to all analyzed parameters, differences between subjects were not significant (t -test, $P > 0.12$).

Fig. 3 shows the onsets of pursuit changes and saccades for the two conditions. Factor N vs. T was statistically highly significant ($P < 0.001$). The low correlation coefficient ($R^2 = 0.01$) shows that onsets of pursuit changes and saccades were independent for the N condition, whereas they were strongly correlated ($R^2 = 0.91$)

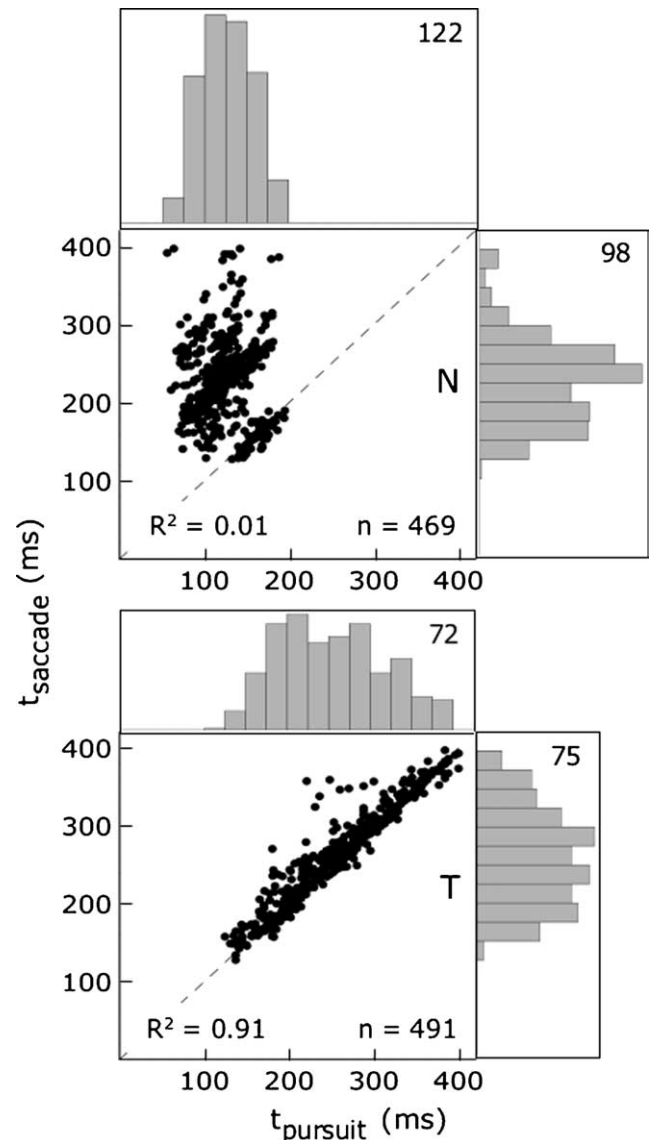


Fig. 3. Saccade latency (t_{saccade}) plotted against pursuit latency (t_{pursuit}) for the N and T conditions. Dashed lines indicate $\Delta t = 0$ (synchrony), n the number of data points and R^2 the linear correlation coefficient. Latency distributions are shown in bins of 25 ms. Numbers indicate the maximum number of data points per bin.

for the T condition. Changes of pursuit started 125 ± 30 ms after target onset for the N condition. These values are in agreement with latencies of 109 ± 21 ms reported by Engel, Anderson, and Soechting (1999). Saccade onsets were 229 ± 55 ms after target onset for the N paradigm. The mean latency of 229 ms is slightly longer than previous reports of about 200 ms (Engel et al., 1999; Leigh & Zee, 1991). For the T condition, saccade onsets were 260 ± 62 ms after target onset. Onsets of pursuit changes occurred 254 ± 63 ms after target onset. For the T condition, latencies of pursuit changes and saccades were 129 ms and 31 ms longer than their respective latencies for the N condition. The distributions of pursuit and saccade latencies were

significantly different from each other for the N condition ($P < 0.001$), but not for the T condition ($P = 0.08$).

The computed pursuit directions were used to derive two angles indicated by $\Delta\phi_{\text{pre}}$ and $\Delta\phi_{\text{post}}$. Angle $\Delta\phi_{\text{pre}}$ was defined as the direction of pursuit just preceding the first saccade after the new target's onset ($\phi_{\text{pursuit_pre}}$) relative to the old target's direction of motion ($\phi_{\text{target_old}}$). Angle $\Delta\phi_{\text{post}}$ was defined as the direction of pursuit just after the first saccade after the new target's onset ($\phi_{\text{pursuit_post}}$) relative to the new target's direction of motion ($\phi_{\text{target_new}}$). The angles $\phi_{\text{pursuit_pre}}$ and $\phi_{\text{pursuit_post}}$ were computed as means over periods of 32 ms (grey bars in Fig. 1B), $\phi_{\text{pursuit_pre}}$ ending 20 ms before and $\phi_{\text{pursuit_post}}$ starting 40 ms after the onset of saccades (t_{saccade}). The chosen time periods warranted that beginning and end of saccades were not treated as pursuit signals. The guarantee is based on the measured relationship between duration and amplitude of saccades (Collewyn, Erkelens, & Steinman, 1988) showing that saccades smaller than 5° last less than 35 ms.

Pursuit direction $\phi_{\text{pursuit_pre}}$ is plotted against the old target's direction of motion $\phi_{\text{target_old}}$ in the left panels of Fig. 4. Angle $\Delta\phi_{\text{pre}}$, being $\phi_{\text{pursuit_pre}} - \phi_{\text{target_old}}$, indicates the angular deviation of pursuit relative to the old target's direction of motion. $\Delta\phi_{\text{pre}} = 0$ if the data points are lying along a slope of one, which means that the eyes pursue the old target without deviation. Fig. 4 shows a

distinction between the results for the N and T conditions. Factor N vs. T was highly significant ($P < 0.001$). Pursuit angle was moderately correlated with the old target's directions of motion for the N condition ($R^2 = 0.55$), indicating that pursuit often changed to the direction of the new target's motion before the onset of saccades. The high correlation coefficient ($R^2 = 0.92$) and the mean latencies for pursuit and saccades for the T condition show that, on average, the eyes pursued the old target until shortly before saccade onset. Computed means and SDs of $\Delta\phi_{\text{pre}}$ were $-1^\circ \pm 21^\circ$ for the T condition, showing that the eyes pursued the old target fairly accurately.

In a similar way, the right panels of Fig. 4 show $\phi_{\text{pursuit_post}}$ plotted against $\phi_{\text{target_new}}$. Correlation coefficients were high ($R^2 > 0.91$), showing that, after saccades, the eyes pursued the new target fairly well in both conditions. Condition (N vs. T) was statistically a significant factor ($P < 0.001$). Means and SDs of $\Delta\phi_{\text{post}}$ were $0^\circ \pm 30^\circ$ for the N condition and $-2^\circ \pm 18^\circ$ for the T condition. These values indicate that the eyes pursued the new target's direction somewhat better in the T condition. Apparently, removal of the old target had a slightly negative effect on the quality of pursuit after saccades. The high correlations for Δt , $\Delta\phi_{\text{pre}}$ and $\Delta\phi_{\text{post}}$ in the T condition show that pursuit changed fast from old to new targets, namely, within saccades.

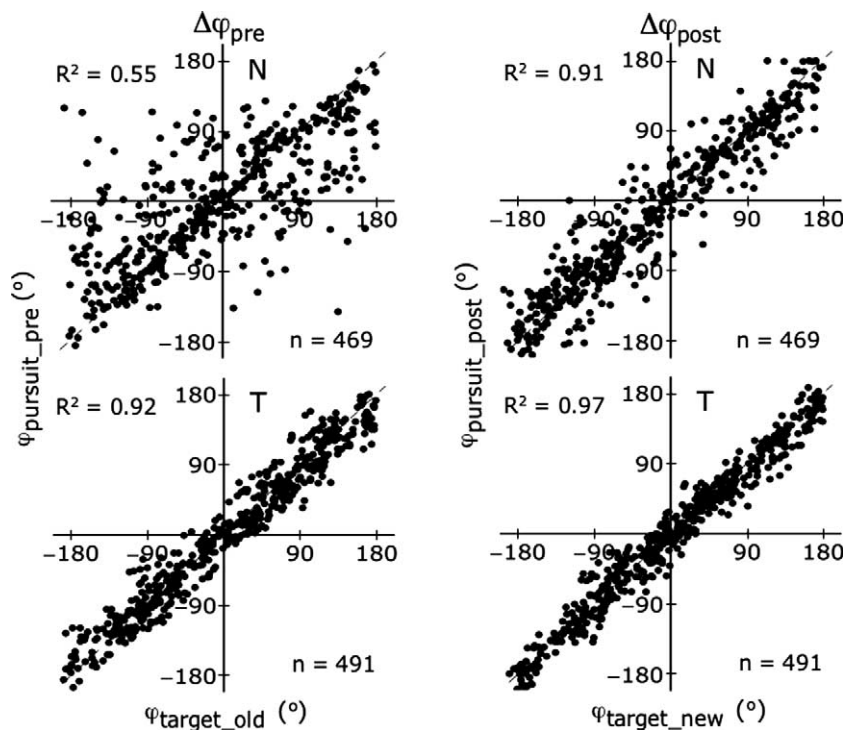


Fig. 4. Pursuit direction ($\phi_{\text{pursuit_pre}}$ and $\phi_{\text{pursuit_post}}$) plotted against the target's direction of motion ($\phi_{\text{target_old}}$ and $\phi_{\text{target_new}}$) for the N and T conditions. Dashed lines indicate $\Delta\phi_{\text{pre}} = 0$ or $\Delta\phi_{\text{post}} = 0$ (no deviation between pursuit and target direction), n the number of data points and R^2 the linear correlation coefficient.

4. Discussion

4.1. Previous research

Pursuit and saccades have been extensively studied for the N condition. Usually stimuli were called ramp or step-ramp stimuli in this condition. Main findings of these studies were that latencies of pursuit were considerably shorter than those of saccades (Adler et al., 2002; Engel et al., 1999; Krauzlis & Miles, 1996a; Krauzlis et al., 1999) and that random variation was uncorrelated between both types of responses (Merrison & Carpenter, 1994). Latencies of pursuit changes and saccades and their correlation measured in this study for N stimuli (Fig. 3, top panel) were in agreement with these findings. Pursuit direction after the saccades (Fig. 4, right panels) was somewhat better matched to the new target's direction of motion than reported by Engel et al., 1999, who found mismatches that depended on the angle between old and new target's directions of motion. The better matches may be related to differences in target speeds used in the two studies. Speeds were below 12 deg/s in the present study and between 15 and 30 deg/s in the study of Engel et al., 1999. It may be that overcoming big changes in pursuit velocity requires more time than just the duration of small saccades. Inspection of Figs. 2 and 7 of a study that analyzed catch-up saccades during sustained pursuit (De Brouwer, Missal, Barnes, & Lefevre, 2002) support this interpretation. The figures show that directional errors were considerable for high target speeds and virtual absent for low speeds.

A problem for interpretation of the present results is that target motion affects size and latency of saccades. For catch-up saccades it has been demonstrated that target motion changes saccade size (De Brouwer, Missal, & Lefevre, 2001; Gellman & Carl, 1991; Keller & Johnsen, 1990; Ron, Vieville, & Droulez, 1989). Dependence of saccades on target velocity has also been reported for saccadic latency (Kanai, van der Geest, & Frens, 2003; Tanaka, Yoshida, & Fukushima, 1998). Due to these relationships it is not possible to compare individual responses to changes in target speed and direction. To minimize effects on means and variances as much as possible, target steps, speeds and directions have been chosen randomly from the same pool in the conditions N and T. The measured difference between the mean saccadic latencies of saccades in the two conditions was 31 ms. Fortunately the difference is small in comparison with differences in pursuit latencies and, therefore, cannot be an alternative interpretation of the results.

4.2. Coordination of pursuit and saccades

How are pursuit and saccades synchronized? Are they already synchronized at the level of saccade preparation

or is synchronization limited to the level of saccade execution? Gardner and Lisberger (2001, 2002) reported evidence for a tight coupling between the pursuit and saccadic systems at the level of target selection. These authors examined natural eye tracking tasks that consisted of orienting saccades and tracking pursuit eye movements. They reported behavioral (Gardner & Lisberger, 2001) and physiological (Gardner & Lisberger, 2002) evidence for a serial organization, indicating that commands for pursuit target selection are mediated by saccade execution signals. The mean latencies measured in the N and T conditions may give insight in the possible organization of pursuit and saccade generation (Fig. 5). As has been mentioned before, mean latencies of pursuit changes (118 ms) and saccades (229 ms) were in agreement with reports of the literature for the N condition. The obvious interpretation of these latencies is that changes in pursuit and saccades are induced simultaneously by target onset and that the mean difference of 111 ms reflects differences in processing time. Mean latencies were longer for the T condition, which indicates that in this condition the decision to switch to another target took more time than in the N condition. However, if latency increases reflect decision time, and thus target selection, one would expect that decision time affected pursuit and saccade latencies by similar amounts. This was not the case. Mean latencies of pursuit increased by 129 ms and mean latencies of saccades by 31 ms (Fig. 5A). If we suppose that the increase in saccadic latency reflects decision time, then preparation

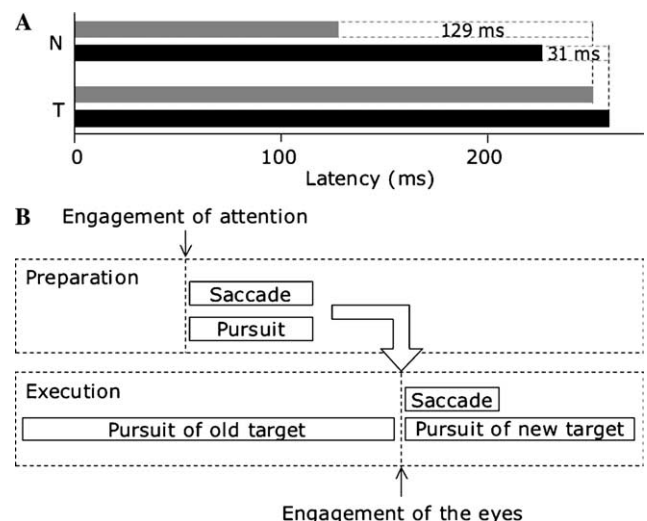


Fig. 5. (A) Mean latencies of pursuit changes (grey) and saccades (black) for the N and T conditions. Dashed bars indicate time differences between latencies in the N and T conditions. (B) Flow diagram for the generation of synchronous pursuit changes and saccades. Preparation starts by engagement of attention to the new target while the eyes remain engaged to the old target. After some time, the saccade is executed and the eyes are engaged to the new target by transfer of the computed signals to the oculomotor system.

of pursuit changes did not start at decision time, but $129 - 31 = 98$ ms later.

4.3. A mechanism for pursuit and saccade coordination

How can we model coordination of pursuit and saccades? The simplest idea is to assume that saccades are prepared from the time that the decision to pursue another target is made and that preparation of pursuit starts after another dead time of about 98 ms. This model explains the onset latencies, however, it does not explain the fast pursuit changes in the T condition. Due to the delayed onset of pursuit preparation, pursuit would still be changing after the saccades. An alternative hypothesis is presented in Fig. 5B. According to this idea control of pursuit and saccade occurs in two stages called preparation and execution. Preparation of saccade and pursuit change start together by engagement of attention to the new target. In the meantime, the eyes pursue the old target because at the execution level the pursuit system remains engaged to the old target. Preparation ends when control parameters are computed for both pursuit and saccade. The computed information is transferred to the execution level resulting in disengagement from the old target and execution of the saccade and the change in pursuit. Such a two-stage mechanism explains the synchronized pursuit and saccadic responses as well as the fast pursuit changes in the T condition. Furthermore, it may explain why pursuit changes and saccades were not synchronized in the N condition. The explanation may be that, at the execution level, the pursuit system was prematurely disengaged from the old target. As a consequence, pursuit started prematurely.

A two-stage mechanism for saccade and pursuit generation supposes an internal degree of freedom, namely, the execution time of saccades and pursuit. If this time were under voluntary control, the mechanism for saccade and pursuit generation would be usable for covert orienting. Human beings have the ability of covert orienting, i.e. to visually attend one location while the eyes remain locked on another location. The underlying mechanism is still controversial. Posner and Petersen (1990) proposed an independent attention system. In contrast, Rizzolatti and colleagues (Rizzolatti, Riggio, Dascola, & Umiltà, 1987; Sheliga, Riggio, & Rizzolatti, 1994) argued that attention employs the circuits used for motor control. Very recently, Smith, Rorden, and Jackson (2004) presented evidence for the role of the eye-movement system in covert orienting. They showed impaired spatial attention in a neurologically healthy subject who could not make eye movements as a result of congenital impairment. The two-stage mechanism for saccade and pursuit generation could be a good candidate for covert orienting.

Acknowledgments

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