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Prediction of saccadic amplitude during smooth pursuit eye movements ☆

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Abstract

If humans try to pursue a moving target, the nervous system uses predictions to overcome some of the nervous systems delays. It is therefore possible for the eyes to pursue a target with virtually no delay and to make accurate catch-up saccades to moving targets. Another example of a delay is the latency of a saccade made in response to a target step. Due to imperfect pursuit, the retinal error will change during this latency. The aim of the present study was to investigate whether step-induced saccades take into account this change. To vary this change in retinal error, the gain of the pursuit eye movement was manipulated successfully by adding a patterned background in one condition and a concomitant hand tracking in another. The increased gain of the pursuit eye movements in the hand tracking condition significantly modified the change in retinal error during the latency. However, no significant differences in saccadic amplitude were found between conditions. We conclude that these step-induced saccades are generated independently of the gain of the pursuit eye movement. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Our everyday environment contains a multitude of moving objects. If a human observer wants to watch such a moving target, he or she will make voluntary pursuit eye movements in order to keep the object of interest on the fovea, the central area of the retina where visual acuity is high. Although the velocity of the pursuit eye movement is typically closely related to that of the target (for a review, see Carpenter, 1988), the smooth pursuit gain is generally found to be smaller than unity (e.g., Murphy, Kowler, & Steinman, 1975; Collewijn & Tamminga, 1984) and the observer has to initiate high velocity, saccadic eye movements to maintain foveation (e.g., Stark, Vossius, & Young, 1962).

These "corrective saccades" are characterized by the fact that both eye and target are moving when the saccade is planned and made. In research on the interaction between pursuit and saccadic eye movements, two other types of saccades have been studied. In experiments using the step–ramp paradigm (Rashbass, 1961), the target moves smoothly, but the eye is initially stationary. In experiments using the flashed-target paradigm (introduced for pursuit eye movements by McKenzie and Lisberger, 1986), the eye moves smoothly, and a saccade is made towards a stationary target. Saccades in these three different conditions (corrective, step–ramp, and flashed-target) may use different sources of information.

One of the main questions of interest has been which sources of information are used to make saccades while pursuing a target. Participants could use purely retinal information, directly related to the mismatch between the movements of eye and target. Alternatively, participants combine retinal with extra retinal information to obtain estimates of the motion of the target in space, and combine this information with estimates of the movement of the eye. In this paper, we will discuss three sources of information: two retinal sources and one extra retinal source.

The primary source of information is the retinal error: the retinal distance between target and fovea. As information about the retinal error can only be used after a certain delay (i.e., the latency of the saccade), it is useful to predict a future error using the motion of the target relative to the retina. For this prediction, information based on the target's retinal velocity (second source: retinal slip) could be used in principle. Another possibility is to use extra retinal information on the pursuit eye movement itself for this prediction (third source). As the pursuit eye movement is partly based on predictive information (Becker & Fuchs, 1985; van den Berg, 1988), using an efference copy of the motor command would allow for the use of these predictive capacities (Brenner & Smeets, 1998). Note that if participants draw on such extra retinal information to make predictions of the retinal error, they also need information (or assumptions) on the target motion relative to the head. Many other combinations of information sources could also be used to make the prediction of the error that develops during the latency of the saccade.

With regard to the first source of information (the retinal error), the central question of interest has been at which point in time this error is sampled. The saccadic amplitude must be determined after the step occurs and more than 80 ms before the beginning of the saccade, since visual information on target location is unable to affect the saccade when presented in the last 80–100 ms preceding saccade onset (e.g., Becker & Jürgens, 1979). Some empirical evidence within the step–ramp paradigm (e.g., Heywood & Churcher, 1981; Keller & Johnsen, 1990) indeed suggests that saccades are based principally upon a position error sampled around 100 ms prior to the saccade (see also Rashbass, 1961; Robinson, 1965).

As to the second source of information (retinal slip), it is evident that the target must be observed for a certain minimum amount of time before target velocity has been measured (Smeets & Brenner, 1994) and can be taken into account. Speed information about target motion *can* be used for the generation of saccades with latencies as short as 150 ms (e.g., Vieville, Ron, & Droulez, 1987; Ron, Vieville, & Droulez, 1989; Keller & Johnson, 1990), but is not always used (Heywood & Churcher, 1981).

Unfortunately, experiments on the contribution of the third source of information (extra retinal information on the pursuit eye movement) using the step–ramp paradigm have yielded inconsistent results. In a study by McKenzie and Lisberger (1986), two of three monkeys ignored the intervening pursuit eye movements while initiating saccades to briefly flashed targets, which led them to suggest that saccades are generated on the basis of retinal error only. On the other hand, Schlag, Schlag-Rey, and Dassonville (1990) showed that the saccadic system accounted for the pursuit movement if the flash was presented for a longer time. The amount of compensation in their experiment differed considerably between monkeys. Also for humans, various authors (Gellman & Fletcher, 1992; Ohtsuka, 1994; Zivotofsky, Rottach, Averbuch-Heller, Kori, Thomas, DellOsso, & Leigh, 1996; Herter & Guitton, 1998) reported that saccades are (partly) compensated for intervening pursuit eye movements.

The interpretation of experiments using the flashed-target paradigm is not without pitfalls. A first problem is that the motion of the flashed target is ambiguous: information on target velocity is absent in the experiments. As this information is required to plan an adequate saccade, participants have to make an assumption. If they assume that the flashed target moves with the eye (which is perfectly reasonable: its afterimage does so), a saccade towards the position of the retinal error is adequate. On the other hand, if the participant assumes that the target is stationary relative to the head, the retinal error has to be corrected for the intervening pursuit eye movement to be adequate.

A second problem with interpreting flashed-target experiments is that it is not self-evident that the saccade is planned in retinal co-ordinates (e.g., Karn, Møller & Hayhoe, 1997). If the saccade is, for instance, directed towards the perceived location of the flash relative to the location of the moving target at that instant, the saccade will be affected by the systematic errors in the perception of this location (Nijhawan, 1994; Brenner & Smeets, 2000).

A third problem in understanding those studies is that to make an accurate saccade, knowing the speed of the eye relative to the flashed target is not enough. To estimate the saccadic amplitude, the pursuit speed has to be combined with the actual latency of the saccade relative to the flash (or step), which is highly variable (Carpenter, 1988). Ignoring this variability in latency will lead to considerable errors in the planning of the saccade. For instance, if the pursuit movement is at 10°/s, a saccade with a latency of 300 instead of 200 ms makes an error of 1°. When analyzing behavior, this error can also be interpreted as an underestimation of the gain of the pursuit by 33%. So, even if the pursuit is perfect and known to the saccadic system, an error in the timing of the saccade leads to an error which appears to be due to problems in the use of pursuit information.

To circumvent these problems, we designed a paradigm in which information on the speed of the saccadic target was always present and highly predictable. In our experiment, the stimulus for the smooth pursuit movement was a sinusoidal moving target. The saccade was elicited by a displacement of the complete stimulus. If the eye follows the target perfectly, it would – after a saccade of exactly the same size as the displacement – follow the target again perfectly without any modifications of the pursuit movement. Thus, for this stimulus, the latency of the saccade would have no *direct* effect on the required size of the saccade.

When the pursuit is not perfect, two factors will affect the required size of the saccade. The first factor is the delay (phase lag): if the eye follows the stimulus with a certain delay, the retinal error will be larger when the stimulus displacement is in the same direction as the pursuit than when they are in opposite directions. The second factor is the gain: if the gain is not one, the amplitude of the saccade required to come on target will also depend on the latency. If the gain is smaller than unity and the stimulus steps at a zero-crossing, the required amplitude will increase until the stimulus has reached its extreme position, and then decrease again. Note that the effects of manipulating the gain are independent of whether saccades are planned in retinal or spatial coordinates. In both coordinate systems, the nervous system has to take into account information about the gain of the pursuit eye movement to generate saccades that come on target.

The major aim of our study is to investigate the interactions between the saccadic and pursuit components of eye movements using this paradigm. More specifically, we hope to shed some new light on the question whether the ensuing saccade takes information on the smooth pursuit eye movement into account or not. An essential concept of the present experiment is to manipulate the smooth component of the pursuit eye movement while keeping the target stimulus signal constant over all conditions. The smooth pursuit eye movement has been found to be affected by two manipulations: the presentation or absence of a patterned background and the performance or absence of a concomitant hand tracking movement. The reason for investigating the presence of a patterned background is that a stationary background is known to reduce the gain of steady-state eye smooth pursuit velocity signal significantly (e.g., Collewijn & Tamminga, 1984; Masson, Proteau, & Mestre, 1995). The reason for introducing an additional manual motor task was that simultaneous hand tracking has been found to increase the gain of the steady-state smooth pursuit eye-velocity signal significantly (e.g., Steinbach & Held, 1968; Steinbach, 1969; Mather & Lackner, 1981; Koken & Erkelens, 1992).

In sum, the purpose of the present study was to investigate whether saccades within a ramp–step–ramp paradigm take into account the error that builds up during their latency. In order to do so, the gain of the pursuit eye signal is manipulated while exactly the same target motion is used in all conditions. If saccades are generated independently of the pursuit eye signal, saccadic amplitudes to a target step should be insensitive to the pursuit gain manipulations as employed in this study. On the other hand, if saccades are initiated while taking into account the gain of the pursuit signal, the employed manipulations should lead to considerable effects on saccadic amplitude sizes (see Fig. 1). With a lower gain, the retinal error during the latency would be increased for steps in the direction of the pursuit, and decreased for steps in the opposite direction. The predicted size of this effect for

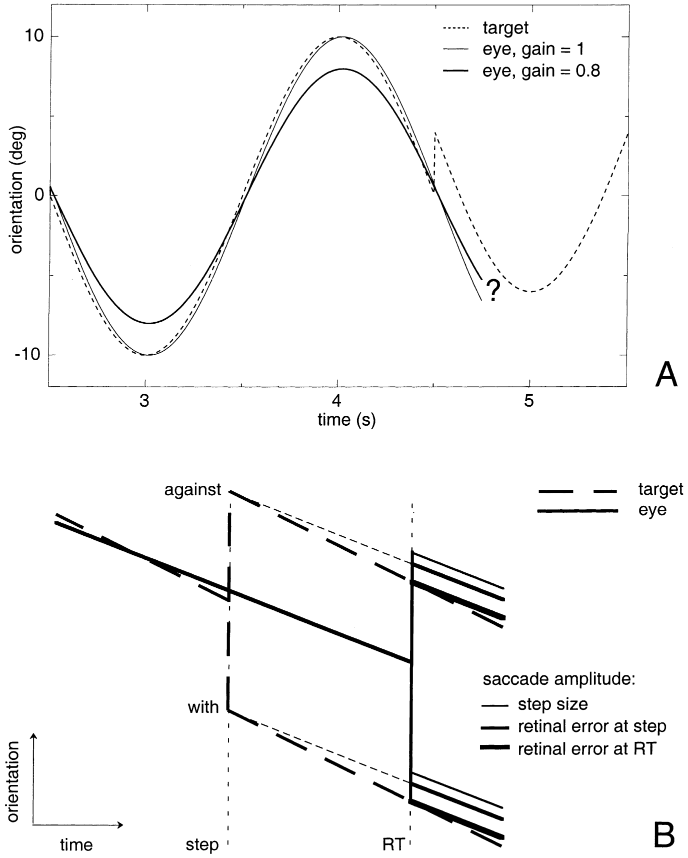

Fig. 1. Effects of pursuit gain on the amplitude of saccades. (A) The eye tracks a sinusoidally moving target (dashed curve) with a pursuit gain of 1 (thin curve) or 0.8 (thick curve) and a delay of 20 ms. At $t = 4.5$ s, the target steps 4° against its smooth movement direction. Due to delay of pursuit, the retinal error is slightly smaller than 4°. About 250 ms latency, the eye will make a saccade towards the target. At that latency, the size of an adequate saccade depends clearly on the gain of the pursuit eye movement: 3.5° for pursuit with a unity gain, but only 2.2° for pursuit with a gain of 0.8. We show only the smooth component of the pursuit movement; the retinal errors in the analysis are based on the composite eye movement. (B) Differences in saccadic amplitudes for the two possible directions of the target step and three possible sources of information. The saccade is adequate if both the retinal error and the error that builds up during the latency of the saccade are taken into account.

a 200 ms saccadic latency and a 10% gain change is about the same size as the differences in saccadic amplitude which will be caused by the (always present) about 20 ms delay of the pursuit. Although our experiments showed a clear effect on the saccadic amplitude due to the delay of the pursuit, we found no effect of the manipulations. We conclude, therefore, that the gain of the pursuit is not taken into account when saccades are made in response to a target step.

2. Methods

2.1. Participants

Eleven undergraduates served as participants in a single session, which took less than one hour. They were all right-handed and all had normal, uncorrected vision. Participants were naive with respect to the purpose of the experiment and were each paid DM 12 for participation.

2.2. Apparatus

Testing was conducted in a dark room. Participants were seated in front of a screen at a distance of 150 cm. The stimulus device was a He–Ne laser, which projected a 3 mm diameter point target onto the screen. The horizontal position of the target was varied by means of a servo-controlled mirror galvanometer.

The head was supported by a chin-rest (ASL). We did not immobilize the head (using a biteboard), to let the participants perform the task as comfortably as possible. Moreover, fixating the head is known to change the dynamics of saccades (Collewijn, Steinman, Erkelens, Pizlo, & van der Steen, 1992). Left-eye orientation was monitored with an IRIS (Skalar) infrared eyetracker. This system records eye orientation by reflection of iris-sclera boundaries by means of infrared light (Reulen, Marcus, Koops, de Vries, Tiesinga, Boshuizen, & Bos, 1988). The analogue output from the IRIS (bandwidth DC-100 Hz) was digitized at a rate of 1000 Hz. The overall accuracy for the eye movements was better than 0.5°. However, as we did not immobilize the head, participants could reposition their heads, which sometimes caused offsets in the eye-signal. We compensated for such offsets.

In the active hand movement conditions, participants were requested to slide a knob in accordance to the left–right target movement. The knob was connected to a linear movement registration system (Potentio Recti RH 28/300; TWK Elektronik GMbH) which measured the movements of the right hand with an accuracy of 0.1 mm at a rate of 1000 Hz. We used the hand data only to check whether participants had followed the instruction to move.

2.3. Experimental paradigm

Each block of trials started with a calibration procedure of the IRIS in which the participant had to fixate sequentially three positions on a horizontal line for one second; both extreme positions (at 10° eccentricity) were fixated three times, the central position six times. This calibration was followed by 10 trials of 16 s in which participants were asked to track the target with their eyes (see Fig. 2). The target moved sinusoidally at a frequency of 0.5 Hz with peak-to-peak amplitude of 20°. In every trial, the target stepped twice: one step of 4° randomly to the left or right and a second step of 4° in the opposite direction. The direction of the second step relative to the stimulus motion (with or against) was independent of the direction of the first step. These steps always occurred when the target crossed the central position (maximal target velocity). The first step occurred after 4–8 s of tracking (randomly varied); the second 4–8 s later. Each block of trials thus contained 20 target steps, randomly in the same direction as the smooth movement or opposite to that direction. After the step, the smooth target movement continued as before the target step.

We presented four blocks of trials, each using a different condition. The conditions were presented in a random order. In two conditions, the target was tracked with the eyes only. In one of them, the room was completely dark, so that only the laser dot was visible. In a second condition, the room was dimly illuminated and participants tracked the laser beam while it moved over a patterned background (an array of 142×36 squares of 0.14°, colored randomly black or white). In two other conditions, participants in addition had to track the laser beam with a concomitant hand movement (again with and without presenting the patterned background). Participants did not receive any visual feedback of their hand movements; they had to rely on their ability to map visual and kinesthetic information to track the target with their hand.

2.4. Data analysis

For the interpretation of the data, we split the signal in two components: smooth pursuit eye movements and saccades (Fig. 2(B–E)). We started with

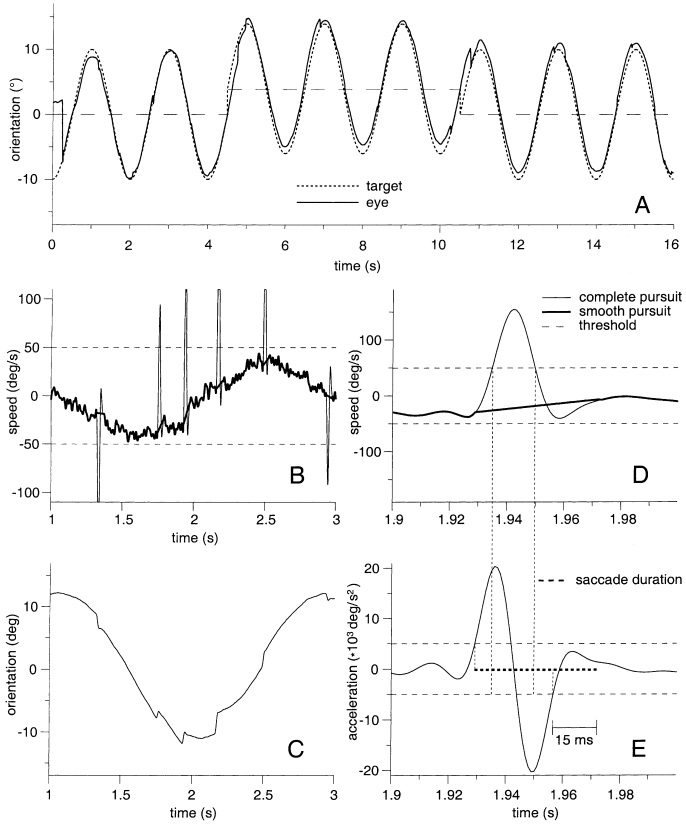

Fig. 2. Example trials. (A) Raw data of target and eye movement of the first trial of participant #2 in the condition without hand movement in the dark. At $t = 4.5$ s, the target steps 4° with the smooth movement; 6 s later (at $t = 10.5$ s) the target steps 4° against the smooth movement. (B–E) Part of the first trial of participant #7 in which the pursuit was poor. Graphs show the determination of saccade duration and the removal of a saccade from the pursuit signal. (B, C) The speed and orientation of the eye. The speed signal (thin curve) surpasses the thresholds six times in 2 s of pursuit. By removal of the six saccades, the smooth component of the pursuit is obtained. (D, E) Speed and acceleration around the third saccade. The initial estimate of saccade duration is based on the conservative velocity threshold. Using the acceleration threshold, the determination of onset and offset were refined. Finally, an additional 15 ms were included at the end. To obtain the smooth component of the pursuit, the saccades are replaced by the interpolated speed (B, D).

converting the eye movement data into degrees using the calibration measurement and low-pass filtering (50 Hz). To detect saccades, we used both a velocity threshold (50°/s) and an acceleration threshold (5000°/s^2). The velocity threshold was used to make a first estimate of the onset and end of the saccade: the period in which the eye moves faster than the velocity threshold.

Subsequently, we added the periods before and after reaching the velocity threshold in which the eye acceleration or deceleration was above threshold. To minimize effects of post-saccadic drift on the remaining pursuit signal, we included in our definition of the saccade an additional 15 ms after the end of the saccade. If the resulting duration was more than 35 ms, we treated the signal in this period as a saccade, otherwise as noise in the smooth pursuit eye movement.

For the calculation of the characteristics of the smooth pursuit signal, we calculated the velocity of the eye and target. To obtain the smooth component of the movement of eye and target, we removed saccades and the target step from the velocity signals and replaced them by an interpolation of the velocity. Gain, maximum cross-correlation, and delay of the smooth pursuit component of the eye movement were calculated from these smooth velocity signals using a fast-Fourier technique (Press, Flannery, Teukolsky, & Vetterling, 1987). We restrict our analysis to trials in which participants pursued the target more or less sinusoidally. We therefore excluded trials in which the maximum cross-correlation between pursuit and target was less than 0.7.

Saccades in response to a target step have latencies above 100 ms (e.g., Fischer & Ramsberger, 1986). We therefore determined for each target step the first saccade that occurred more than 100 ms after that step. If this saccade had an inappropriate amplitude (<1° or >10°) or latency (>800 ms), we assumed that it was not a response to the target step and excluded this step from further analysis. These requirements reduced the number of saccades per participant we could analyze. For two participants, more than 10% of the saccades were excluded; these participants were dropped from analysis. The data in the results section are based on 670 saccades made by nine different participants.

We cannot use the eye movement during the saccade as a measure of the amplitude of the saccade, because the pursuit eye movement continues during the saccades. Therefore, saccades in the same direction as the pursuit appear to be larger than saccades in the opposite direction (Jürgens & Becker, 1975). To characterize the saccade, we defined the measure “net saccade amplitude”. This is the eye movement during the saccade minus the estimated smooth pursuit component of the eye movement (obtained by integration of the interpolated eye velocity). This measure has the advantage that it does not depend critically on the definition of the onset and end of the saccade: using a wider definition will add smooth pursuit eye movement to the raw amplitude, but not to the net saccade amplitude. This justifies our 15 ms safety margin in our definition of the saccade end.

To correlate the saccadic amplitude with the error at the time of the target step, we need a measure for the retinal error. As we were not able to determine the absolute orientation of the eye reliably (see Section 2.2), we had to make an estimate of the head orientation. This estimate is based on the assumption that the eye follows the target without systematic left–right asymmetries; we attribute systematic left–right errors to head movements. As the participant can have moved his/her head anywhere within a trial, we used the shortest time to estimate the left–right error: one period of the sine. We corrected the composite eye orientation data (pursuit including saccades) for this head movement. Using these corrected eye movement signals, we calculated the retinal error at the time of the step and the onset of the saccade.

The data were analyzed in a 2 (eye-only, eye-and-hand) $*$ 2 (dark or patterned) $*$ 2 (pursuit in same or opposite direction than step) $*$ 2 (left or right target movement) ANOVA. We will use a significance level of $P = 0.05$ to determine whether differences are significant.

2.5. Predictions

The eye will not be in the same orientation and moving at the same speed in each trial. To test different sources of information presumably used for the generation of the saccade quantitatively, we predicted the saccade goal for each target step. The three information sources mentioned in Section 1 can be specified and combined in many ways. For instance, the retinal error can be taken at any moment between the step and the saccade. We chose to restrict ourselves to four models, each based on the actual combination of eye and target motion for that target step.

For the first model, we assume that the goal is the retinal error at the time of the saccade. This is, of course, not a prediction the brain can make, as this information is not present before the initiation of the saccade. The three other models are based on sources of information the nervous system may have used. For the second model, we take the retinal error at the time of the step as the predicted goal. According to the last two models, the goal is the sum of the retinal error at the moment the target steps and an estimate of the error introduced by the imperfect pursuit during the latency of the saccade. In the third model, we estimate this error by the product of retinal slip velocity (just after the target step) and the latency of the saccade. This estimate assumes that the velocity of eye relative to target remains constant during the latency. In the fourth model, we estimate this error by the actual target movement during the latency (presumably predicted) multiplied by one minus the gain of the pursuit eye movement. The first two models are illustrated in Fig. 1(B). As the last two models approximate the error at reaction time, their predictions will be closer to the first than to the second model.

Using these four models, we calculate a predicted goal of the saccade for each target step. As saccades to stationary targets systematically miss these targets, the predicted saccade amplitude differs in two respects from the predicted goal. Saccades typically cover 90% of the distance to be covered (for jumping targets, Lemij & Collewijn, 1989), so the predicted saccade amplitude is 90% of the distance to the predicted goal. Secondly, temporally directed saccades are 0.2–0.3° larger than nasally directed saccades (Collewijn, Erkelens, & Steinman, 1988). Combined with the fact that we measured the orientation of the left eye, we predict that saccades to the left undershoot the target 0.25° less and saccades to the right 0.25° more.

3. Results

3.1. Gain and delay

We first checked whether our manipulations had the predicted effect on the gain of the smooth pursuit eye movements (Fig. 3). The ANOVA showed a significant ($P < 0.0001$) main effect for movement condition, indicating that the gain for the pursuit signal was higher in the eye-and-hand tracking condition than in the eye-only tracking condition, 0.99 and 0.90, respectively. A smaller but significant ($P < 0.01$) main effect was also found for background condition, indicating a lower gain for the pursuit signal when a patterned background was visible than in the dark, 0.92 and 0.96, respectively. No further main or interaction effects were found.

The delay of the pursuit was on average 21 ms. The ANOVA showed that this delay did not differ significantly between conditions.

3.2. Latencies

The latency of the saccade depended on various parameters of the target step (Fig. 4). The largest significant main effect was found for step direction: eye latencies were longer when the target step was opposite to the smooth target motion than when both were in the same direction (302 vs. 230 ms; $P < 0.0001$). Furthermore, latencies were slightly longer when the eye moved

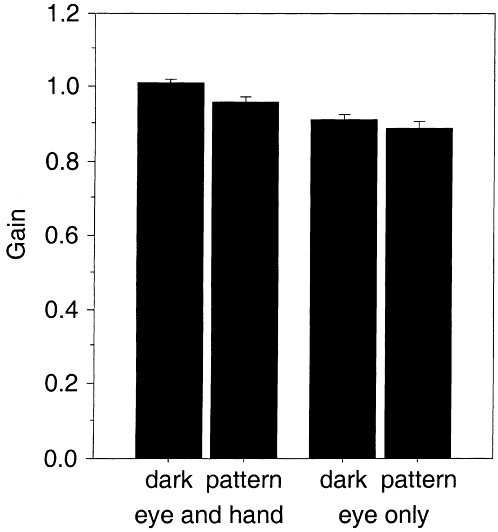

Fig. 3. Gain of the smooth pursuit eye movement component for the four different tracking conditions. Error bars indicate the standard error.

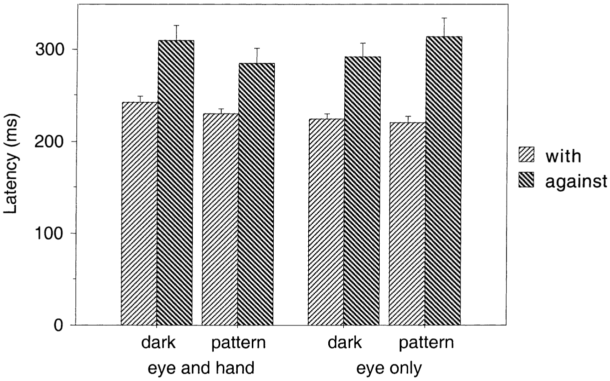

Fig. 4. Latencies of saccadic eye movements in the four experimental conditions for the two directions of the saccade. Thin striped bars: The target step is in the same direction as the smooth target movement; thick striped bars: the step opposite to the smooth target movement.

to the right (258 vs. 245 ms; $P < 0.005$). This is caused by measuring the orientation of the left eye only and the fact that temporally directed saccades are somewhat faster than nasally directed saccades (Collewijn, Erkelens, & Steinman, 1995). The ANOVA showed that besides these main effects only interaction effects with sign (left–right) were significant.

3.3. Saccade amplitude

Fig. 5 shows that saccadic amplitudes were larger (4.21°) when the target step was in the same direction as the smooth target motion than when it was in the opposite direction (2.89°). Not visible in the figure is that saccades to the left were 0.5° larger than those to the right. This is caused by measuring the orientation of the left eye only and the fact that temporally directed saccades are somewhat larger than nasally directed saccades (Collewijn et al., 1988). The ANOVA showed indeed significant ($P < 0.0001$) main effects for pursuit direction and for sign – left or right. Except for these two highly significant effects, no other main or interaction effects were found. The experimental manipulations (hand movement and background) that changed the gain of the pursuit thus had no effect on the amplitude of the saccade.

3.4. Information sources

As we argued in the introduction, the amplitude of an accurate saccade is the sum of the retinal error and a pursuit-related term. Fig. 6(A) shows that the retinal error immediately after the target has stepped 4° is in general not 4°. When the step is in the same direction as the smooth movement the retinal error is larger (4.60°) than when the step and smooth movement are in the opposite direction (3.14°). This difference is mainly due to the 21 ms delay in tracking the target: this delay corresponds to an error of 0.65° at the moment

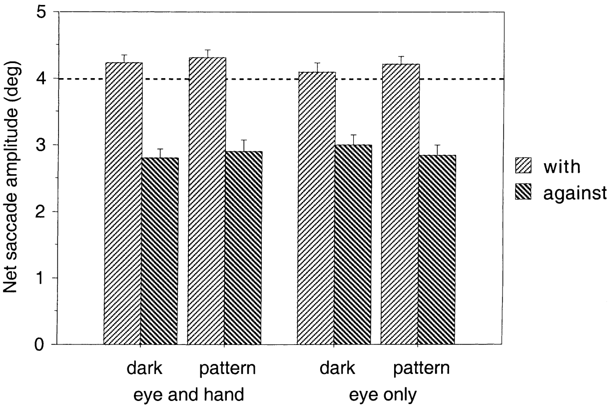

Fig. 5. Net amplitudes of the saccades made after the 4° target-step (indicated by the dashed line) in the four pursuit conditions for both directions of the saccade.

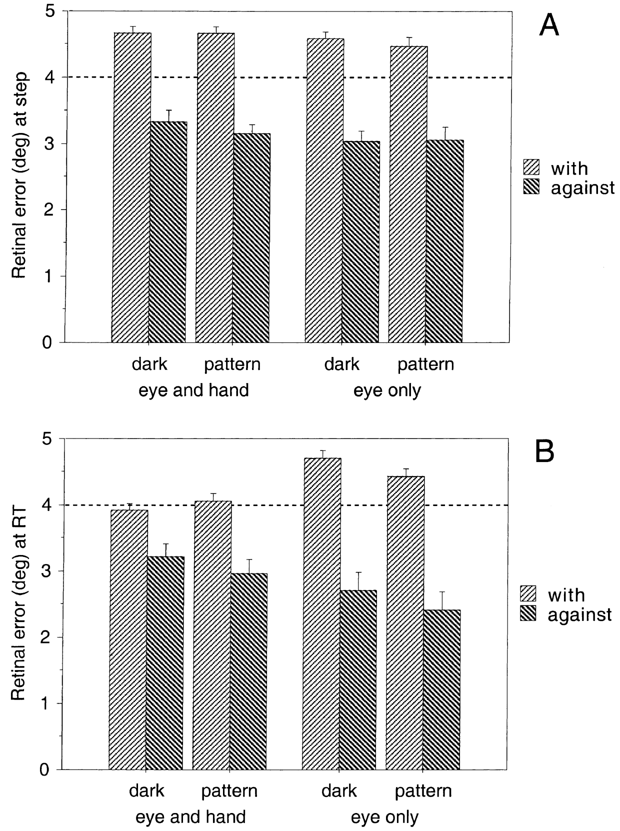

Fig. 6. Retinal error measured at two moments during pursuit for the four pursuit conditions and the two directions of the saccade. (A) Retinal error of the target immediately after the 4° step (dashed line). (B) Retinal error at the onset of the saccade (RT).

of the step. The ANOVA indeed showed a significant ($P < 0.0001$) effect for pursuit direction. No other main or interaction effects were found.

The difference of 1.46° in retinal error between the two directions of target step is almost the same as the observed difference (1.32°) in size of the actual saccades initiated in response to the target step (cf. Figs. 5 and 6). In addition, the ANOVA for both variables shows no main effect for the experimental manipulations (hand movement and background) that changed the gain of the pursuit movement.

The development of the retinal error during the latency of the saccade, however, was affected by one of the manipulations, as revealed by the retinal error at the time of the saccade in Fig. 6(B). Again, a difference between the two directions is visible (as in Fig. 6(A)), but the retinal errors differ more from the step amplitude in the conditions with a low gain (without hand movement). The ANOVA showed indeed a significant ($P < 0.0001$) effect for pursuit direction and a significant ($P < 0.0001$) interaction between pursuit direction and hand movement. No other main or interaction effects were found, indicating that the relatively small effect of background on the pursuit gain (see Fig. 3) did not lead to significant effects on the development of the retinal error during the latency of the saccade.

To make a more quantitative comparison of the observed saccadic amplitude with the expected retinal errors under the different experimental conditions, we compared predictions based on four models for the saccade amplitude with the amplitude itself (see Section 2.5). The results of these predictions are shown in Fig. 7. For clarity, we grouped the two conditions

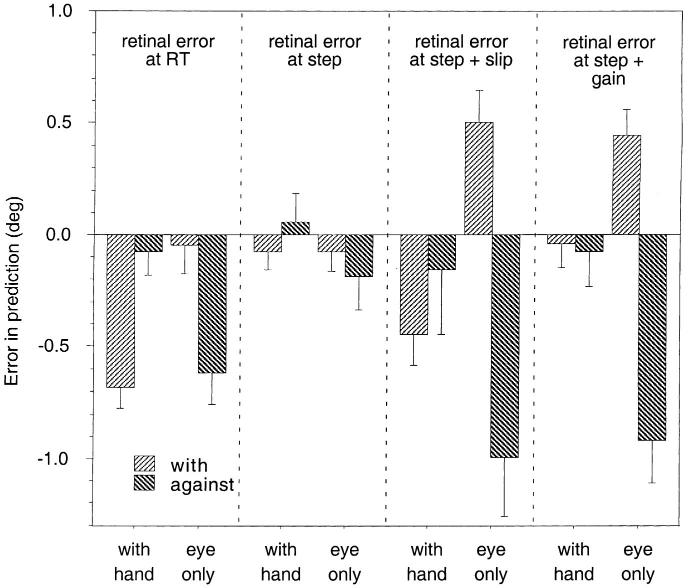

Fig. 7. Errors in predicting net saccade amplitude for various information sources. Predictions are calculated separately for the conditions with and without hand tracking. The net amplitude of the saccade differs systematically from the amplitude predicted based on the retinal error at the onset of the saccade. However, if the retinal error just after the target step is used as information source, the saccade amplitude is predicted without systematic errors. Adding more information (retinal slip or the error in pursuit caused by a low gain) introduces systematic errors in the prediction.

with the highest gain (eye-hand tracking) and the two conditions with the lowest gain (eye-only tracking), as the small difference in gain due to the background had no significant effect on the development of the retinal error. It is clear that (in line with the previously mentioned findings) the retinal error just after the step yields predictions without any systematic errors ($P < 0.05$). For all other ways of predicting the saccade amplitude, the predicted and actual amplitudes differed significantly in at least two conditions.

4. Discussion

We successfully modified the gain of the pursuit eye movement signal by two manipulations. A 10% higher gain was found when a hand-tracking component was added to the task and a 5% lower gain was found when a patterned background was visible behind the target signal. The main result is that these manipulations induced *no* significant changes in saccadic amplitude size. In order to check whether this finding is consistent with the notion that saccades are based on the retinal error as only source of information (and to exclude the possibility that the effect is too small to measure), we predicted saccade size using different sources of information for each target step. The predictions of saccade amplitude assuming that either retinal slip or the gain of the pursuit eye movements has been included in the saccade programming processes differ up to 1° from the measured amplitudes (see Fig. 7). Since these effects were larger than the 0.6° effect of the delay on the retinal error, which was clearly visible in the saccade size, we have no doubt that our measurements were accurate enough to determine these effects. We can conclude that saccades in response to a target step during pursuit are determined independently from the pursuit eye movement component.

4.1. Determination of saccadic eye movements

Our question which information is used to generate saccades is closely related to the much-debated question which frame of reference is used. In experiments on this issue, participants initiated a saccadic eye movement to a shortly flashed target while the eyes were moving smoothly before making a saccade to the flashed position. The amount of compensation for this intervening smooth movement varied considerably between experiments (see Section 1). In our experiment, we found that a difference in gain level of the pursuit component does not influence the saccade size. This suggests that also in a ramp–step–ramp paradigm saccades are determined independently of the gain of the smooth pursuit eye movement. If this is true, the determinant of the saccade is not the smooth movement made by the eye, but rather the movement the participant or monkey intended to make (following the perceived motion of the target, Zivotofsky et al., 1996). This suggestion is an additional explanation for the differences in the results obtained in the experiments we discussed in Section 1.

4.2. Initiation of saccadic eye movements

Although this was not the primary concern of our study, we found various systematic effects of stimulus conditions on the latency of the saccade. Latencies were shorter when a saccade was initiated in the same direction as the target movement as compared to the opposite direction. There are several possible interpretations for this result, which is a reproduction of an effect recently reported by Tanaka, Yoshida, and Fukushim (1998). This phenomenon resembles that of inhibition-of-return (Dorris, Taylor, Klein, & Munoz, 1999). It might be possible that a target step is perceived faster when it occurs in front of the target (or in the same retinal hemifield) than behind the target (or in the opposite retinal hemifield). Some theories of spatial visual attention suggest that pre-setting a motor program in one direction, like in a pursuit eye movement tracking condition, would also pre-set covert attentional motor programs in that direction, (see, e.g., Rizzolatti, Riggio, Dascola, & Umilta, 1987; Sheliga, Riggio, & Rizzolatti, 1994). Another possible explanation is that pre-setting the pursuit system in one direction facilitates all eye movements in the same direction, or inhibits the initiation of all eye movements in the other direction. This explanation assumes a connection between the pursuit and saccadic eye systems with regard to their motor output (see Krauzlis, Basso, & Wurtz, 1997).

4.3. Nature of saccades during pursuit

Our main finding is that the amplitude of the saccades in response to an unpredictable target step are independent of the gain of the pursuit eye movement during the time between step and saccade. We do not argue, however, that the gain of the pursuit is not known or cannot be taken into account when making a saccade. Moreover, some saccades during pursuit have to depend on the gain of the pursuit.

For example, Koken and Erkelens (1992) observed that the average delay between eye and target when pursuing a sinusoidally moving target is independent of the contribution of saccades to the eye movement. When pursuing a target which moves at high frequency (>1 Hz), the gain of the smooth eye movement drops to values close to 0. The loss of smooth pursuit is compensated by an increasing number of saccades ensures that the gain of the composite eye movement remains well above 0.5. Nevertheless, the delay remains as short as 30 ms (Koken & Erkelens, 1992). In other words: since the substitution of pursuit by saccades did not increase the average delay between the movement of target and eye, the saccades have to be caused by a mechanism which can predict a future error. This prediction has to be based on some knowledge of target motion and pursuit gain. Therefore, it might even be the case that at a typical latency before the saccade, no retinal error exists. A nice example is provided by the first large saccade in Fig. 1 of Koken and Erkelens (1992). This saccade occurs at $t = 450$ ms. The figure shows that the retinal error starts to develop in the direction of that saccade only after $t = 350$ ms. Thus there was no retinal information related to the actual saccade at a plausible time before that saccade.

In sum, some saccades during pursuit are highly predictive in nature, and presumably use information on the pursuit-gain to accomplish this prediction. Probably, both these saccades and pursuit are based on the same positional information (van Gelder, Lebedev, & Tsui, 1995; Krauzlis et al., 1997). However, not all saccades share the information with the pursuit eye movements. For instance, the saccades induced by the unpredictable steps in our experiment, for instance, showed no sign of prediction. So saccades during pursuit can be divided in (at least) two categories: either driven by the retinal error, or being part of the (predictive) pursuit mechanism. A similar distinction between visually guided and non-visually guided saccades during pursuit has been proposed by van Gelder, Lebedev, and Tsui (1997).

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