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# Intentionally-evoked modulations of smooth pursuit eye movements

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## Abstract

When observers pursue a moving target with their eyes, they use predictions of future target positions in order to keep the target within the fovea. It was suggested that these predictions of smooth pursuit (SP) eye movements are computed only from the visual feedback of the target characteristics. As a consequence, if the target vanishes unexpectedly, the eye movements do not stop immediately, but they overshoot the vanishing point. We compared the spatial and temporal features of such predictive eye movements in a task with or without intentional control over the target vanishing point. If the observers stopped the target with a button press, the overshoot of the eyes was reduced compared to a condition where the offset was computer generated. Accordingly, the eyes started to decelerate well before the target offset and lagged further behind the target when it disappeared. The involvement of intentionally-generated expectancies in eye movement control was also obvious in the spatial trajectories of the eyes, which showed a clear flexion in anticipation of the circular motion path we used. These findings are discussed together with neurophysiological mechanisms underlying the SP eye movements.

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## 1. Introduction

When primates observe a moving stimulus they generally make smooth pursuit (SP) eye movements in order to keep the target within the fovea. In contrast

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to saccadic eye movements, SP eye movements are assumed to occur only when a moving stimulus is visible. Correspondingly, SP movements could not be executed while tracking imaginary or acoustic stimuli in the dark (Buizza, Leger, Berthoz, & Schmid, 1979; Gauthier & Hofferer, 1976). From these results it was concluded that the SP movements are guided by visual feedback of actual target characteristics only. In contrast to those results, several researchers observed that it is possible to initiate SP eye movements before the target starts to move (Barnes & Donelan, 1999; Kowler & Steinman, 1979) or to maintain them for some time after the target has vanished (Becker & Fuchs, 1985; Mitrani & Dimitrov, 1978). This pattern of results indicates that the oculomotor system like other sensorimotor systems is not only guided by visual feedback, but takes into account the observer's expectations and predictions of future target positions.

The aim of the present study is to investigate the spatial and temporal characteristics of SP eye movements with respect to the predictability of a movement. Different sources that modulate SP eye movements can be distinguished: (1) external stimulus characteristics like movement velocity and trajectory and (2) internally-generated information when the observer is able to control certain characteristics of the stimulus movement. In particular, in this study the role of internal information is investigated in an eye-tracking task with or without intentional control over the target offset. In the induction condition the target offset is generated unexpectedly by the computer whereas in the intention condition the target offset is controlled by the observer's button press. The findings of several studies lead to different hypotheses concerning the temporal and spatial features of SP eye movements under those conditions.

Becker and Fuchs (1985) showed that human subjects (as non-human primates, cf. Eckmiller & Mackeben, 1978; Whittaker & Eaholtz, 1982) were able to bridge gaps when the target disappeared briefly. In their experiments observers were instructed to continue tracking when the target disappears. In these continuation experiments the SP velocity started to decelerate 200 ms after the target disappearance to a residual velocity of approximately 60% until the target reappeared. In addition, Mitrani and Dimitrov (1978) demonstrated that without an instruction to continue the pursuit movements the eyes did not stop immediately when the target had vanished. In their study the eye velocity returned to zero within 300–600 ms after the stimulus vanished. Moreover, these experiments showed that the delay or drift-time depended on movement duration and on the probability of target disappearance. Therefore, it can be concluded that the overshoot could not be based only on ballistic inertia of the eyes. Instead, the results indicate an automatic generation of anticipations, which provide the input for eye movement planning and execution.

The spatial characteristics of a target movement are also anticipated by SP eye movements. For example, Suh, Leung, and Kettner (2000) investigated the ocular behavior with a gap and a perturbation task while tracking circular movements. The two-dimensional eye trajectories looked similar for the gap and the non-gap condition. Also with perturbations in a horizontal or vertical direction the eyes overshoot the unexpected directional change and continued along the anticipated cir-

cular path for about 94 ms until a correction moved the eye smoothly in the new direction.

Up to now, it remains unclear whether the anticipations are computed exclusively on the basis of external visual information or whether they are modulated by intentional factors as well. Several models described the SP system as a closed-loop negative-feedback system and neglected the contribution of factors like predictions and intentions (for an overview see Pola & Wyatt, 1991). The role of intentional information is supported in a study by Steinbach (1969), who observed that the accuracy of eye-tracking was improved if the visual target was moved actively by the observer's hand. Under those conditions, SP movements were possible even in the dark. On the basis of these results, Vercher et al. (1996) and Vercher, Lazzari, and Gauthier (1997) proposed a model containing a coordination control system, which receives signals from the eye-tracking and the arm motor system. As a result of these coordination control systems, the dynamics of the SP system are changed when the arm and target motion are correlated. In the same way as the internal representation of the visual stimulus movement is used the internal representation of the arm movement could be used to improve the performance on the basis of predictions.

The first aim of the present study is to further investigate the influence of observer's target control on SP eye movements. The results of Vercher et al. (1996) and Vercher et al. (1997) indicate that the exchange between signals of different motor systems could provide information which leads to more accurate SP behavior during maintenance. An increased accuracy might also be observed for the termination of SP behavior, when the target disappeared as a consequence of an internally-generated button press (intention condition). The discrete button press is a much simpler motor task than the observer induced target motion used by Vercher and it contains only the time information when movement is stopped. The interesting question is whether or not under these conditions the tendency to stop pursuit in advance prevails over the tendency to maintain pursuit. Results in favor of the tendency to maintain pursuit would suggest an automatic generation of mainly stimulus-driven predictions; results in favor of the tendency to stop pursuit in advance would suggest at least an internal modulation of these predictions.

The second aim of the present study is to investigate the stimulus dependent predictive component, which could be based on an internal representation of the stimulus movement. A stimulus will be presented moving with a constant velocity on a circular but highly predictable trajectory. This trajectory is used in order to collect more information about the trajectory-specific programming. With linear movements one cannot distinguish between a trajectory-specific or rather spatially unspecific inertial overshoot. With circular pursuit movement all eye muscles are involved and therefore a more complex programming is necessary. It is expected that the eye movement trajectories continue at a circular path after the stimulus disappearance and therefore provide evidence for an internal representation of the stimulus path. In the following we tested these ideas.

## 2. Method

### 2.1. Participants

Eight students of the University of Munich were paid to participate in the experiment. They reported normal or corrected-to-normal vision and were naive as to the purpose of the experiment.

### 2.2. Apparatus and stimuli

The experiment was carried out on a PC and the stimuli were presented on a 17 in. color monitor with a refresh rate of 75 Hz. The participant's head was placed on a chin and forehead rest 500 mm in front of the monitor. Eye movements were measured by a SMI eye link infrared video based eye-tracker. Each eye was measured with an infrared digital camera respectively. The reflection pattern on the cornea of each eye of two infrared light emitting diodes mounted beside each camera was measured by the cameras. By isolating the pupil position the point of gaze could be calculated in *XY* coordinate pairs. The eye movements were sampled at a rate of 250 Hz. Before each block the system was calibrated by offering nine saccadic targets on the monitor. During the experiment, the calibration was adjusted online and if necessary a drift correction was performed automatically in order to correct the drift in the calibration. The room was dimly lit.

The moving stimulus was a dot of  $0.5^\circ$  (4.35 mm).<sup>1</sup> On each trial, the dot traced-out a trajectory that circled around a fixation cross at a radius of  $6.1^\circ$  visual angle (53.3 mm, cf. Fig. 1). The angular velocity of the stimulus was realized by shifting the dot  $2.14^\circ$  clockwise with every vertical retrace of the monitor (13.33 ms per frame), resulting in the angular velocity of  $160.2^\circ/s$ , which corresponds to a tangential velocity of  $17^\circ/s$  (149 mm/s). This target velocity was well within the velocity range in which observers can accurately track a moving target (Robinson, Gordon, & Gordon, 1986).

The movement started at the upper part of the circle (in a range of  $20^\circ$  before and  $20^\circ$  behind the 12 O'clock position), and angular movement distance varied from  $90^\circ$  to  $360^\circ$  with the absolute movement times of 560–2240 ms.

### 2.3. Design and procedure

Two different instructions (induction and intention) were presented blockwise and the order was counterbalanced between participants. Observers were instructed to

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<sup>1</sup> If the description contains the degree scale only, the unit refers to the corresponding angle in respect to the circle! If scales giving both degree and millimeter are used, the units refer to the corresponding angle in respect to the eye.

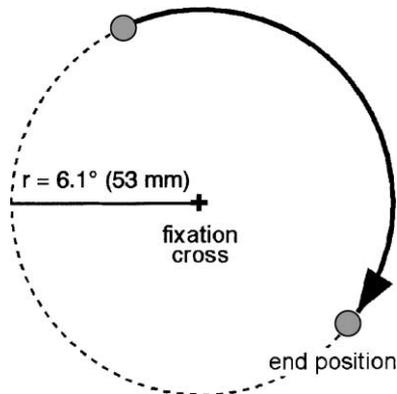


Fig. 1. Stimulus configuration used in the present experiments. The moving stimulus circled the central fixation cross at a radius of  $6.1^\circ$  (53 mm).

follow the target with the eyes until it vanished. Nevertheless, the central fixation cross was visible throughout the experiment as the starting point for the eye movement. Each trial began with an auditory warning signal before stimulus onset and the fixation cross changed its color from red to green when the target appeared. In the induction condition the experimental program induced the offset of the moving stimulus. In the intention condition the participant was instructed to press a button with the right index finger in order to stop the target's motion. Observers were asked to stop the movement at an arbitrary point after the stimulus had moved  $90^\circ$ , yet before it had moved  $360^\circ$ . Moreover, they should distribute stop positions between these virtual markers and should try to avoid recurrent salient positions. If the subject pressed the button too early or too late, an error message was presented, and the trial was repeated immediately. When the stimulus vanished the participant should stop the pursuit movements and return to the fixation cross when its color changed from green to red.

Participants were confronted with 30 repetitions within each cell of the complete within-subject design, that is, overall with 60 trials. The experiment lasted approximately 30 min, including the calibration, training trials and short breaks.

#### 2.4. Data analysis

The eye movements were analyzed offline by using MATLAB 5.0 scripts. Movement parameters were analyzed for each subject and each trial. The offset of the pursuit movement was defined as the point in time when a saccade was made back to the fixation cross (which was the instructed way to end pursuit). In order to calculate the overshoot the vanishing point of the target was marked within the data. The onset of saccades was defined as the point in time when ocular velocity exceeded  $35^\circ/\text{s}$  and the acceleration exceeded  $9.500^\circ/\text{s}^2$ .

### 3. Results and discussion

#### 3.1. Overshoot

The overshooting score on every trial was computed as the angular difference between the eye position at the time the moving stimulus disappeared and the eye position at the time the pursuit movement ended by a saccade back to the fixation cross in the center. The values represent displacements expressed in visual angle, that is, the angles between the lines from the center of the circular stimulus trajectory to the eye position at the time of stimulus disappearance and from the center to the end of pursuit. Positive values indicate that the eyes continued after the target disappeared, negative values indicate that the eyes stopped moving before the stimulus disappeared. For segregation of outliers all values below  $-6^\circ$  and above  $6^\circ$  were excluded first (five trials of 451) and then within subjects all values were discarded above or below the criterion of two standard deviations (31 trials). Mean eye position errors were computed separately for every participant and each condition.

With both induction and intention a reliable positive eye position different from zero was observed, that is, the eyes continued to move after the stimulus vanished in both conditions (induction:  $3.10^\circ$ ,  $s_e = 0.14$ ,  $t(7) = 22.02$ ,  $p < 0.001$ ; intention:  $1.50^\circ$ ,  $s_e = 0.21$ ,  $t(7) = 6.98$ ,  $p < 0.001$ ; always two-tailed). Nevertheless, in the intention condition this overshoot was largely reduced and a  $t$ -test revealed a significant difference between the intention and induction condition ( $t(7) = 7.95$ ,  $p < 0.001$ ; cf. Fig. 2). Therefore, the prediction of the self-generated vanishing point enables eye movements to stop faster and to attain greater spatial accuracy. Also the standard deviation within participants was smaller in the intention condition, which is further evidence for the improved accuracy. This difference is not significant, but it shows a weak statistical tendency (induction:  $0.67^\circ$ ,  $s_e = 0.11$ ; intention:  $0.57^\circ$ ,

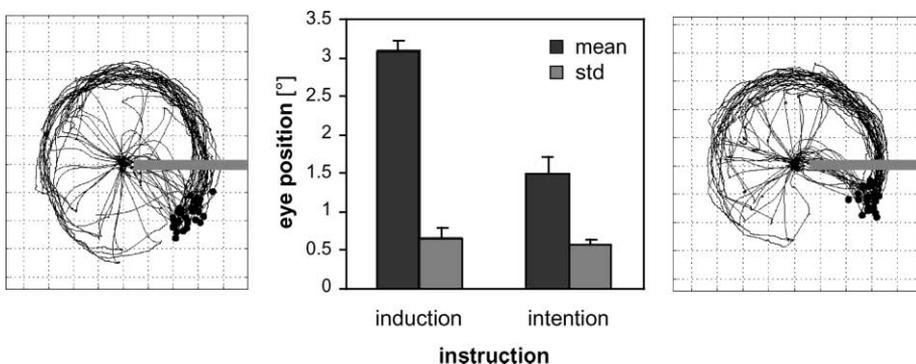


Fig. 2. (Middle) Eye position at the end of pursuit as a function of instruction (induction vs. intention). The dark bars represent the mean values, and the light bars, the standard deviation. Positive values indicate errors in the direction of movement, negative values errors opposite to the direction of movement. Error bars represent standard errors between participants. (Left and right) Trajectories of one subject for the induction (left) and intention (right) condition.

$s_e = 0.07$ ,  $t(7) = 1.42$ ,  $p = 0.2$ ). In addition to the mean values, Fig. 2 shows all eye traces of one subject, where the traces are rotated to map the position of stimulus disappearance at the 3 o'clock position (see gray line). The figure nicely shows the different amount of overshoot in both conditions and also illustrates the slightly reduced variance of final eye position in the intention condition.

### 3.2. Spatial lag or lead

In order to investigate the spatial position of the eye in relation to the target, we computed the difference between the stimulus offset position and the eye position when the target disappeared. So as to obtain a comparable measure for each eye movement trial, eye positions, which did not always correspond exactly to the stimulus path, were projected to the stimulus trajectory. The values reported below represent degrees of visual angle along the stimulus trajectory. Negative values stand for a spatial lag and positive values denote a spatial lead of the eyes in relation to the stimulus. For segregation of outliers first all values below  $-3^\circ$  and above  $3^\circ$  were excluded (37 trials of 451) and then within subjects all values above or below the criterion of two standard deviations (22 trials).

The data show an average spatial lag in both conditions, that is the eyes lagged behind the stimulus (induction:  $-0.5^\circ$ ,  $s_e = 0.07$ ,  $t(7) = 7.41$ ,  $p < 0.001$ ; intention:  $-0.8^\circ$ ,  $s_e = 0.14$ ,  $t(7) = 5.87$ ,  $p = 0.001$ ; cf. Fig. 3). Although these lags are statistically different from zero the absolute amount of these lags is rather small. This is more obvious if these values are transformed to show the temporal lag of the eye: in the induction condition the eyes lagged the stimulus by 29 ms and in the intention condition by 47 ms. These average lags lay well below 100 ms, that is the assumed reaction time of the pursuit system (Lisberger & Westbrook, 1985). Thus, these small lags show that there must be a predictive component within the eye movements,

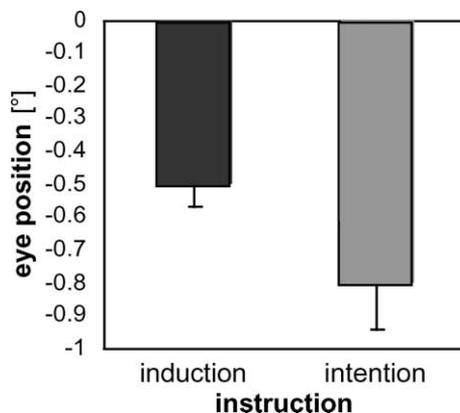


Fig. 3. Spatial position of the eye at stimulus offset as a function of instruction (induction vs. intention). Positive values indicate a spatial lead, negative values a spatial lag. Error bars represent standard errors between participants.

because otherwise the eyes could not be phase-locked as was observed here. These results are similar to those of Keating (1991) who found that monkeys lag sinusoidal target movements of 0.4–1.4 Hz by only 7–22 ms.

Nevertheless, in accordance with the reduced overshoot the eyes lag stronger in the intention condition than in the induction condition. A comparison of the mean values did not reveal a significant difference, but a statistical trend was evident ( $t(7) = 2.00, p = 0.085$ ). It is plausible that in the intention condition where the observers can prepare optimally for stimulus disappearance they tend to fall behind the stimulus in order to stop the eye movements appropriately. This pattern seems to rule out the possibility that participants used a strategy where they first searched for a point on the trajectory where they could stop the target when it reached that position.

### 3.3. Gain

The mean gain profiles were computed for each subject and condition. The average profile can be seen in Fig. 4. In the induction condition the gain remained relatively constant at 0.85 until 150 ms after the target disappearance and then declined rapidly to 0.45 in the following 100 ms. In contrast, in the intention condition the gain started to decline 180 ms before the stimulus offset and decelerated to a gain of 0.7 at time 0 and to 0.3 in the following 250 ms. After  $t = 0$ , the gain profiles for the two conditions differ significantly from each other ( $p < 0.05$ ) and in the last 150 ms before stimulus offset show a trend ( $p < 0.10$ ). Within two subjects there was a significant deceleration in the intention condition well before  $t = 0$  (Fig. 4, right). Surprisingly, there was also a significant difference in gain 500 ms before the stimulus offset. That was maybe due to the difference in action control within the conditions: in the induction condition the observer cannot predict the stimulus offset and therefore uses probably a lower gain at the beginning. Nevertheless, in both conditions the gain is around 0.8 for most of the trial and a clear separation occurred not until a

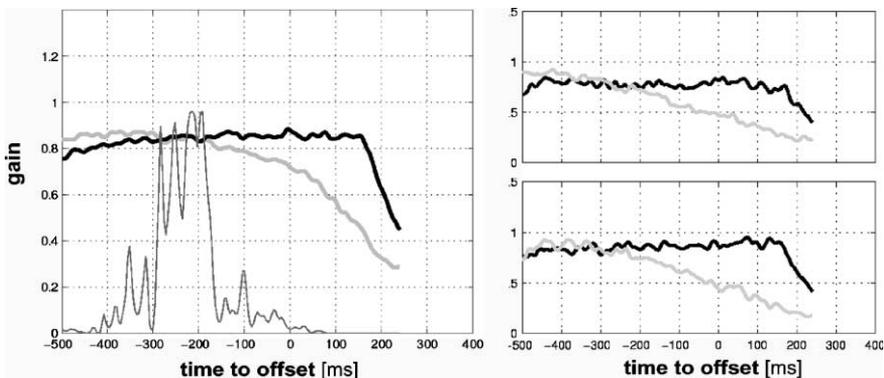


Fig. 4. (Left) Gain of all participants as a function of the induction (black) vs. intention (gray) condition. The thin gray line represents the level of significance for a difference between both conditions. (Right) Gain of two participants with a significant difference between the conditions before  $t = 0$ .

short time before the stimulus offset. Therefore, in the intention condition the lower gain as well as the resulting greater spatial lags described before could only be attributed to the anticipated stimulus offset.

The results show that the intentional control over the target movement provides information, which could be used by the eye movement system in order to stop the SP eye movements more precisely. There seems to be a well-tuned synchronization of button press and eye movement deceleration. It would be plausible if this synchronization does not depend on how the target is stopped, that is, by a button press or other actions. The pure intention to stop the target and the knowledge that the target will stop should be enough to achieve more accurate behavior. In the experiments of Barnes and Donelan (1999), an auditory warning cue was used to initiate the SP eye movement. Therefore, it should be also possible to reduce the overshoot with an adequate external cue (e.g. an auditory cue), where the performance should depend on the time between cue and stimulus disappearance. Nevertheless, we cannot decide on the basis of these data whether there is also a contribution of the exchange of motor commands while triggering the termination of SP movements. Vercher and colleagues (Lazzari, Vercher, & Buizza, 1997; Vercher et al., 1997) showed in their experiments that the eye movement behavior is improved when a tracking movement of the hand produces the stimulus movement. The spatial and temporal accuracy was nearly perfect in terms of gain and phase. The button press in our experiment contains only information about the point of time, when the target vanishes, and it would be interesting to examine the overshoot in an experiment under conditions similar to those of Vercher. It should be noticed that also in the intention condition there still remains an overshoot. Possibly, with a continuous coupling between the observers and the stimulus movements, that is, with additional kinesthetic information, the overshoot could be reduced or even eliminated.

In the induction condition the absolute amount of drift-time lies below the results of Mitrani and Dimitrov (1978) and above those of Suh et al. (2000), both of whom used comparable velocities. Maybe circular movements lead to smaller overshoots than the horizontal movement introduced by Mitrani and Dimitrov, because the circular path requires a more complex programming. In the experiments of Suh et al. (2000), who used also circular movements, the overshoot lasted shorter in comparison to our induction condition, but in their experiments the stimulus changed its direction instead of disappearing and therefore offers visual input for a faster correction. In contrast, in our experiment there is no longer any stimulus input which could be used to correct the eye movements. Therefore the influence of anticipation could last longer.

### 3.4. *Trajectory*

The trajectory of the maintained eye movements after target disappearance show a clear flexion in anticipation of the future target movement. In Fig. 2 this circular overshoot is shown already for one subject. In addition, Fig. 5 shows the flexed eye movements after stimulus disappearance of all subjects in the induction condition. These flexed eye trajectories could rather be explained by a spatial representation

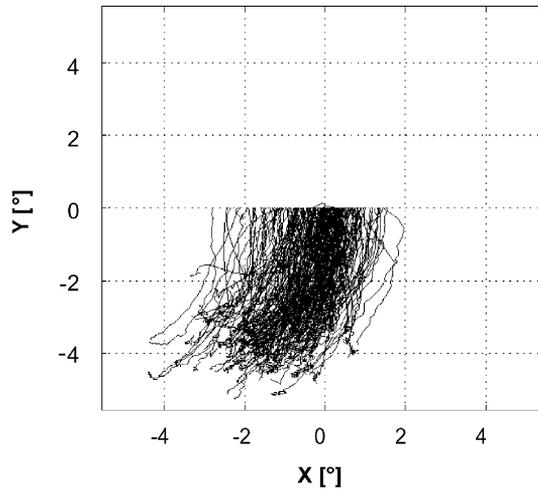


Fig. 5. The eye trajectories of all participants and all trials after the stimulus disappeared.

of the stimulus motion than with a stored efference copy of the last motor command. Otherwise it would have been more likely to find a linear overshoot. The brainstem circuitry controlling the oculomotor nuclei is organized in different neural channels, roughly controlling vertical, horizontal and torsional eye movements separately by three complementary sets of extraocular muscles pulling in the mentioned directions (Carpenter, 1977).

These results resemble those of Suh et al. (2000) where the observers reacted on a change of stimulus direction from a circular to a linear path first with a flexed overshoot in anticipation of the circular movement and then, after delayed reaction time, made corrections toward the linear target movement.

Moreover, the trajectories in Fig. 2 show that in most of the cases, the initial portion of SP showed a radius different from the path of the target. This occurred because the amplitude of the first saccade, which determines the starting point of SP, was somewhat smaller than the radius. It is a well known finding that the initial saccade often undershoots the target position by 10% and that a corrective saccade is necessary in order to bring the target to the fovea (Becker, 1972). Here, it seems that after the saccade a correction is made during SP while shifting the eyes trajectory progressively toward the target's trajectory. This pattern was observed with 6 of the 8 participants and offers additional evidence in favor of an internal representation of target motion, because the eyes began to move on the circular path before they really tracked the target.

#### 4. Conclusions

We compared the spatial and temporal features of predictive eye movements in a task with or without intentional control over the target offset. In the intention con-

dition the eyes showed a reduced overshoot as compared to the induction condition, an increased lag at the end of the movement, and a gain, which started to decline well before the target offset. Additionally, the trajectories of both conditions showed a clear flexion in anticipation of the circular movement path we used.

The overshoot replicated the findings of Mitrani and Dimitrov (1978) that the eyes did not stop immediately when the target vanished. Furthermore, with action control over the target offset, a large improvement could be observed in spatial and temporal components. In the intention condition the overshoot of the eyes was reduced to the half of the induction condition. Accordingly, the eyes started to decelerate well before the target offset and lagged further behind the target when it disappeared. These results are in accordance with the assumed interaction between a prediction mechanism and visual feedback (Becker & Fuchs, 1985). In the induction condition, the observer could react primarily to visual feedback, that is, the disappearance of the target. The system needs a certain time to process this information and to stop the predictive eye movements; the result is an overshoot. Under natural conditions, the observer notices this overshoot and makes a corrective saccade toward the vanishing position (Mitrani, Dimitrov, Yakimoff, & Mateeff, 1979). If the target does not disappear but changes its direction, the new visual input offers opportunity for a correction (Suh et al., 2000). In the induction condition without additional input after target disappearance, the anticipatory influence could maintain for a larger amount of time. In contrast, in the intention condition the observer could start to decelerate the eye movements without visual feedback but with timing information based on the knowledge that the target will disappear with the button press. Moreover, in both conditions the involvement of expectancies based on stimulus characteristics is obvious in the spatial trajectory of the eyes, which shows a clear flexion in anticipation of the circular path after stimulus disappearance as well as a progressing shift of the trajectory in direction of the stimulus path at the beginning of target movement.

The question is now, which mechanism and neural correspondent could account for this pattern of results. Several proposals were made concerning the neural substrate of predictive eye movements. Gottlieb, MacAvoy, and Bruce (1994) described a cortico-ponto-cerebellar circuitry, which underlie the SP system of primates. The middle temporal and middle superior temporal areas MT and MST seem to provide the visual motion information, which is necessary for the target representation. These areas are reciprocally connected with the frontal eye fields (FEF), which are important for the execution of anticipatory eye movements to predictive target movements. In accordance, Barnes and Donelan (1999) proposed that the short-term storage for target characteristics is located in the prefrontal cortex and that the supplementary eye fields may serve as the periodicity estimator, which controls the release of the anticipatory activity through the FEF. MT, MST and FEF are connected via the Basilar Pontine Nuclei with the cerebellum, which is necessary for the execution and maintenance of SP (Ilg, 1997). It was suggested that the cerebellum is also concerned with facilitating the continuation of the anticipatory response (Barnes & Donelan, 1999) or moreover includes a velocity memory in the flocculus (Lisberger, Morris, & Tychsen, 1987). Also the interaction and exchange between

different sensorimotor systems take place at the cerebellum (Vercher & Gauthier, 1988). Suh et al. (2000) found that the neural responses of the flocculus and paraflocculus of the cerebellum were highly correlated with eye movements during the execution of predictive eye movements and concluded that this system generates predictive control during ongoing pursuit. But this result does not exclude the possibility that the flocculus gets its input from a representational system, which is rather independent from the motor execution. Although different proposals reflect an uncertainty about the role of FEF and flocculus all parts of the described circuit are assumed to be necessary for predictive eye movements.

Certainly, all described structures are involved in the emergence of our results, but it is possible to specify mechanisms, which are of particular interest. In both conditions the circular overshoot and the low phase lag indicate the contribution of an automatic SP prediction, that is, a representation of target characteristics. Only in the induction condition is the velocity memory really obvious, because here the gain remains constant for a certain time after the target disappearance. In the intention condition a strong contribution of cognitive expectations lead to a reduced overshoot of the eyes, that is, the knowledge about the dependency between button press and target disappearance leads to reduction of eye velocity advanced to the offset, a greater phase lag at offset time and a smaller overshoot after target disappearance. Therefore, the expectations are used for a more accurate timing of pursuit end.

Nevertheless, also with intentional control in our experiment there still remains an overshoot. There are several possibilities why it is not further reduced or even diminished. First, SP predictions are—at least in parts—an automatic mechanism, which cannot be abolished completely. Second, the motor coupling between button press and eye movements is not strong enough. It is possible that when the observer further controls characteristics of the target's trajectory (e.g. as in the experiments of Vercher, 1996) the overshoot would disappear completely.

Another possibility in order to reduce the overshoot would be to present an external cue which announces the target disappearance. It would be interesting whether similar performance occurs with an extrinsic cue, which offers only timing information without the contribution of exchanged motor components. Nevertheless, also with this method a reduced overshoot would be the result of intentional modulations of SP predictions.

An argument for an automatism of SP predictions is that it facilitates the interaction with the environment by enabling the compensation of delays in the transmission from the retina to the cortex. This has implications not only for motor control but also for the perception of events. It has been observed that the execution of SP eye movements lead to a mislocalizations of the final position of a moving target in direction of the movement (e.g. Kerzel, Jordan, & Müsseler, 2001). Recently we have shown that with intentional control over the stimulus disappearance the overshoot of the eyes as well as the mislocalization in movement direction were reduced to half (Stork, 2002). This result might indicate that eye movements contribute to the spatial representation of objects and that action control is able to affect target localization via a modulation of eye movements (see also Van der

Heijden, Müsseler, & Bridgeman, 1999). Whether there is more evidence for this idea has to be clarified in future research.

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