Anticipatory Gain Modulation in Preparation for Smooth Pursuit Eye Movements

Hiromitsu Tabata, Kenichiro Miura, and Kenji Kawano

Abstract

We studied the effect of the probability of required tracking on the gain of visuomotor transmission for pursuit initiation in monkeys. We recorded the ocular responses to a brief movement (perturbation) of a target located at an eccentric position from the central fixation spot. As soon as the central fixation spot went off, the animal was required to make a saccade to the target if it remained stationary or to track if it moved. The probability of an upcoming ramp motion of the target (horizontal, 20°/sec), requiring pursuit, was varied (target motion probability [TMP] = 0, 0.25, 0.5, 0.75, and 1, which was fixed in a block). We found that the magnitude of the response to the perturbation increased gradually as the TMP increased. The initial pursuit response and the perturbation response showed very similar dependence on the TMP, suggesting that the response to the perturbation could be used as an index of the gain of visuomotor transmission for pursuit initiation. We also found that the changes in the ocular responses after the TMP was changed from one probability to another occurred rapidly (decay constant of only a few trials). These results suggest that the gain of visuomotor transmission in preparing for pursuit is rapidly modulated in accordance with the anticipated future need for pursuit.

INTRODUCTION

Smooth pursuit eye movements are controlled by a visual feedback control system, in which the primary drive signal is target motion on the retina. However, it is also known that extraretinal signals, for example, attentional or cognitive factors, influence smooth pursuit (for a review, see Kowler 1990). For example, expectations about the direction of future target motion produce anticipatory smooth eye movements in the direction of the expected target motion (Kowler & Steinman 1979a, 1979b). Recently, our group reported in monkeys (Kodaka & Kawano, 2003) and humans (Tabata, Hashimoto, Inaba, & Kawano, 2004) that brief movements of a target during fixation induced a larger eye movement when they repeatedly required smooth pursuit than when they repeatedly required fixation or saccade. In other words, the ocular sensitivity to visual motion increases when the subject anticipates forthcoming tracking based on past experiences. These results suggest that the gain of visuomotor transmission before the start of pursuit is influenced by the possibility of future movement.

In the present study, we attempted to characterize the properties of the gain modulation based on the probability of upcoming motion requiring pursuit. We measured ocular responses in two monkeys to a brief movement (perturbation) of a target located at an eccentric position. After disappearance of the central fixation spot, the animals had to make a saccade to the target if it remained stationary or pursue the target if it moved. In Experiment 1, we systematically investigated how the degree of future need for tracking eye movements influenced the gain of visuomotor transmission, by manipulating the percentage of the forthcoming ramp motion of the target (target motion probability [TMP]), requiring pursuit. We found that both the magnitude of the ocular responses to the perturbation and the magnitude of the initial part of the pursuit increased with an increase in the TMP. In Experiment 2, we quantitatively investigated the time course of the changes in the responses to the same perturbation during a transition between two experimental blocks of different TMPs. We report that the response magnitude subsequent to the changes in the TMP changed rapidly over the course of just a few trials. These results suggest that the pursuit system rapidly adjusts the gain of visuomotor transmission in preparing for smooth pursuit in accordance with the anticipated future need for smooth pursuit.

RESULTS

We first examined whether the probability of required pursuit influenced the initiation of smooth pursuit (Experiment 1a; Figure 1A). After the disappearance of the centered stationary fixation spot, monkeys had to either make a saccade (when the eccentric target spot remained stationary) or execute smooth pursuit (when
Figure 1. Schematic diagrams of trials. Each rectangle depicts a snapshot of the screen at a particular moment during the trial. A cross shows the fixation spot and a closed circle shows the target. $p$ shows the percentage of the pursuit trials in a block (TMP). (A) Experiment 1a. The target appeared at a horizontal eccentricity of 2°. The direction of target motion for tracking was randomized in each trial. (B) Experiment 1b. The target appeared at a horizontal eccentricity of 2° and a brief movement of the target (perturbation) was injected before the disappearance of fixation spot. The direction of perturbation and the direction of target motion for tracking were randomized in each trial. (C) Experiment 2. The target appeared 2° above the fixation spot. Although the direction of ramp target motion for tracking was randomized in each trial, the initial target position and the direction of the perturbation were fixed. (D) Two types of TMP sequences in Experiment 2 are shown.

the eccentric target spot moved). Figure 2 shows a comparison between the eye velocity temporal profiles of smooth pursuit in the blocks whose probabilities of target motion requiring pursuit (TMP) were 1 (black line) and 0.5 (gray line). Although the eye velocities in the maintenance phase of pursuit were almost the same, the magnitude of the initial responses in TMP = 0.5 was smaller than that in TMP = 1. The average eye velocities ($\pm SD$) over an 80-msec interval starting from 70 msec after the target motion onset (gray zone in Figure 2) were $8.0 \pm 2.4^\circ$/sec (TMP = 1) and $5.5 \pm 2.0^\circ$/sec (TMP = 0.5). This result suggests that the probability of required pursuit influences the magnitude of the initial driving signal for smooth pursuit. The latency measurements calculated from average temporal profiles were 72 and 78 msec in TMP = 1 and TMP = 0.5, respectively. The small difference in the response latencies might be secondary to the different response magni-
tudes and to the method of measurement. Table 1 shows the quantitative data calculated from pursuit responses in the other direction in this monkey and in another monkey (latency and magnitude of initial pursuit response [sp]). In both cases (Monkey A-R, -L, Monkey B-R, -L), the average eye velocity in TMP = 1 was significantly larger than that in TMP = 0.5 (p < .01, one-tailed t test).

To further study the relationship between the gain of visuomotor transmission for pursuit initiation and the TMP, we recorded the ocular responses to a brief movement (perturbation) of the target during fixation (Experiment 1b; Figure 1B). The intent was to measure the dependence of the gain of visuomotor transmission on the probability of subsequent required pursuit. The upper traces in Figure 3A show the velocity profiles of the ocular responses induced by the target perturbation in the TMP = 0, 0.25, 0.5, 0.75, and 1 blocks. The lower traces in Figure 3A show the velocity profile of the target. The magnitude of the perturbation responses gradually increased with an increase in the TMP. To quantify the response magnitude to the perturbation, we calculated the average eye velocities over an 80-msec interval starting from 70 msec after the target motion onset (gray zone in Figure 3A). The relationships between the magnitude of perturbation responses and the TMPs are plotted as a function of the TMP in four cases.

Table 1. Summary of the Perturbation Responses and the Initial Pursuit Responses

<table>
<thead>
<tr>
<th>Monkey A</th>
<th>Monkey B</th>
</tr>
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<tbody>
<tr>
<td>TMP</td>
<td>R</td>
</tr>
<tr>
<td>Latency (msec)</td>
<td>1</td>
</tr>
<tr>
<td>0.5</td>
<td>69</td>
</tr>
<tr>
<td>sp (deg/sec)</td>
<td>1</td>
</tr>
<tr>
<td>0.5</td>
<td>5.0 (1.6)</td>
</tr>
<tr>
<td>ptb (deg/sec)</td>
<td>1</td>
</tr>
<tr>
<td>0.5</td>
<td>3.1 (0.9)</td>
</tr>
</tbody>
</table>

The values in parentheses are standard deviations. TMP = target motion probability; R, L = rightward and leftward target motion, respectively; sp = initial pursuit response; ptb = perturbation response.

*Data when the TMP = 1 that were significantly larger than the data when the TMP = 0.5 (one-tailed t test, p < .01).
(Monkey A-R, −L, Monkey B-R, −L) in Figure 3B. The data were normalized based on the following equation:

\[ r_{\text{normalized}} = \frac{(r_{\text{TMP} = x} - r_{\text{TMP} = 0})}{(r_{\text{TMP} = 1} - r_{\text{TMP} = 0})} \]

where \( r_{\text{TMP} = x} \) corresponds to the averaged eye velocity in the TMP = \( x \) condition (\( x = 0, 0.25, 0.5, 0.75, \) or 1). It is clear that the increase of the TMP gradually increased the magnitude of the perturbation responses.

To examine whether the probability of required pursuit has a common effect on pursuit initiation and the ocular responses to the perturbation, we compared them under TMP = 1 and TMP = 0.5 conditions (Table 1, “ptb” and “sp”). As described in Table 1, the magnitude of perturbation response (ptb) in TMP = 1 was also significantly larger than that in TMP = 0.5 (\( p < .01 \), one-tailed \( t \) test). Figure 4 shows the relationship between the initial pursuit response (y-axis) and the perturbation response (x-axis) in each monkey. We found the magnitude of perturbation response was strongly correlated with the initial pursuit response in both monkeys (TMP = 1 or TMP = 0.5, rightward or leftward target motion). The similarity of the dependence of the two motor responses on the TMP warranted our adoption of the perturbation response as an index to reveal the gain of visuomotor transmission for pursuit initiation in the following experiment.

In Experiment 2, we examined how rapidly the gain of the visuomotor transmission changed when the TMP changed. Animals were repeatedly exposed to the trial sequence consisting of two types of subblocks whose TMPs were different (Figure 1C and D, see also Methods). We observed sequential changes in the perturbation responses. In Figure 5, response amplitudes to the perturbation are aligned by their trial numbers in the series and averaged over the subblocks. The TMP was changed from 1 to 0 at Trial 0 (identical to Trial 100) and from 0 to 1 at Trial 50 (response amplitudes are plotted as black circles), or the TMP was changed from 0.5 to 0 at Trial 0 and from 0 to 0.5 at Trial 50 (response amplitudes are plotted as gray circles). It is apparent that the response amplitudes were different between the first 50 trials (TMP = 0 subblock) and the last 50 trials (TMP = 1 or 0.5 subblock), and changes in the perturbation responses were observed shortly after the TMP was switched. We fitted an exponential function to the averaged data (solid lines in Figure 5) to quantify the rate of this change. The decay constants for the increases in the ocular responses were 4.5 and 2.6 trials during transitions from TMP = 1 to 0 and from TMP = 0.5 to 0, respectively. The decay constants for the increases in the ocular responses were 4.5 and 2.6 trials during transitions from TMP = 0 to 1 and from TMP = 0 to 0.5. The magnitudes of ocular responses in the steady state in the TMP = 1 and TMP = 0.5 subblocks were 2.1 and 1.5 times larger than the steady-state value in the TMP = 0 subblock. The responses of the other monkey showed similar properties (see Table 2). These results indicate that the change in the gain of the visuomotor transmission occurred in relatively few trials, and the magnitude of the gain depended on the probability of required pursuit.

DISCUSSION

First, we showed that the perturbation response and the initial pursuit response showed very similar dependence on the TMP. This confirms that the ocular responses to the perturbation before initiating pursuit can be used to measure the gain of visuomotor transmission for pursuit initiation. One advantage of observing the perturbation response instead of directly observing the pursuit initiation is that we can measure the gain of visuomotor transmission in TMP = 0, that is, no pursuit condition.
We successfully investigated the transition dynamics of the gain of visuomotor transmission from TMP = 0 to TMP = 1 or 0.5, as shown in Experiment 2, by using this experimental technique.

Second, we found that the ocular responses to the perturbation gradually increased as the TMP increased. In other words, the probability of required pursuit influences the gain of the visuomotor transmission in advance of executing pursuit. This suggests that the pursuit system in preparing for future movements changes the gain of the visuomotor transmission in accordance with the anticipated future need for pursuit. This may be related to the idea that the pursuit system includes an internal or covert signal, such as the “intent to pursue” (Keating & Pierre, 1996).

Third, we found that the gain reached a new level rapidly (decay constants of 2.6–6.7 trials) when the TMP was changed. This gain modulation is much more rapid than the motor learning previously reported in smooth pursuit initiation. Kahlon and Lisberger (1996) demonstrated an increase or decrease in the eye acceleration during smooth pursuit initiation when monkeys were repeatedly presented with targets that moved at one speed for 100 msec and then changed to a second, higher or lower, speed. The decay constants of learning for eye acceleration at 50–80 msec after the onset of pursuit in their two monkeys were 240 trials and 62 trials for experiments designed to increase eye acceleration, and 108 trials and 171 trials for experiments designed to decrease eye acceleration (Kahlon & Lisberger, 1996). Ogawa and Fujita (1997) reported adaptive modifications in postsaccadic pursuit responses. The data in their Figure 3A indicates that a decrease in the initial gain of human smooth pursuit of about 35% needed 200 trials when the subjects were required to track a target that was decelerated from 10° to 2° per second during the catch-up saccade (Ogawa & Fujita, 1997). In contrast to these results, we found that the decay constant of the preparative gain modulation was very short, suggesting

<table>
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<th>Table 2. Quantitative Data from Experiment 2</th>
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<tr>
<td>Monkey A</td>
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<tr>
<td><strong>Time Constant (Trials)</strong></td>
</tr>
<tr>
<td>TMP 0→1</td>
</tr>
<tr>
<td>TMP 1→0</td>
</tr>
<tr>
<td>TMP 0→0.5</td>
</tr>
<tr>
<td>TMP 0.5→0</td>
</tr>
<tr>
<td><strong>Steady-state Gain</strong></td>
</tr>
<tr>
<td>TMP = 1/TMP = 0</td>
</tr>
<tr>
<td>TMP = 0.5/TMP = 0</td>
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Time constants and normalized steady-state gains for each monkey when the TMP was changed.
that it is mediated by a different mechanism from that of the pursuit learning previously reported.

In summary, the results indicate that the pursuit system changes the level of the gain of visuomotor transmission in preparing for pursuit over just a few trials whose steady state is dependent on the probability of required tracking. It has been reported that the perturbation responses during ongoing pursuit are larger than during fixation (Churchland & Lisberger, 2002; Schwartz & Lisberger, 1994). This gain modulation, so-called online gain control, occurs within a single trial dependent on the eye/target state, that is, the gain is low before starting pursuit and becomes high during pursuit (e.g., Krauzlis & Miles, 1996). The gain modulation reported in the present study provides evidence that the gain before starting pursuit is adjusted based on the experiences of several previous trials. This suggests that the initial gain state in the online gain-control mechanism is probably changed through the history of previous trials. The short-term gain modulation based on the recent experiences may contribute to the preparation for future movement in accordance with the minute-by-minute changes in the environment that primates experience.

**METHODS**

Eye-movement data were recorded from two monkeys weighing 7.7 (A) and 7.1 kg (B) (Macaca mulatta and Macaca fuscata, respectively), previously trained to fixate and pursue a small spot. Experiments on Monkey A were conducted at Kyoto University and on Monkey B at the National Institute of Advanced Industrial Science and Technology. All training, surgical, and recording procedures were the same as previously described (Kodaka, Miura, Suehiro, Takemura, & Kawano, 2004; Kawano, Shidara, & Yamane, 1992) and were approved by the Animal Care and Use Committees of both institutions.

Animals faced a tangent screen (80° x 80°) 50 cm in front of the eyes. Two light-emitting diodes (LEDs) were back-projected onto the screen, a centered green one for initial fixation and an eccentric red one to guide subsequent saccade and pursuit. The horizontal and vertical positions of the red LED spot were controlled by a mirror galvanometer system. The presentation of stimuli and the acquisition, display, and storage of data were controlled by the REX system (Hays, Richmond, & Optican, 1982) running on a PC. The data were stored and transferred to another PC for analysis using an interactive computer program based on MATLAB (MathWorks, Natick, MA). Eye-position data were recorded with an electromagnetic search coil system (Datel, Tokyo, Japan) and smoothed with a digital low-pass filter (33 points FIR filter, -3 dB at 80 Hz). We rejected data that included saccades (eye velocity >50°/sec, eye acceleration >2500°/sec²) in intervals of 350 msec starting from 100 msec before the onset of target motion. By these criteria, 5.6% and 23.0% of all data were rejected in Monkeys A and B, respectively.

**Experiment 1**

We designed two types of experiments as depicted in Figure 1A and B: either the no-perturbation (control) condition to observe the smooth pursuit eye movements to ramp target motion (Experiment 1a) or the perturbation condition to observe the ocular responses induced by a brief prior movement (perturbation) of the target (Experiment 1b). Each experiment included two types of trials (pursuit or saccade). The TMP (target motion probability) described the probability of pursuit trial in a block, for example, the TMP = 1 block included only pursuit trials, and the TMP = 0.5 block included equal numbers of pursuit and saccade trials. We used the TMP = 0.5 and 1 blocks in Experiment 1a and the TMP = 0, 0.25, 0.5, 0.75, and 1 block in Experiment 1b. At the beginning of each trial, the animal was required to fixate the stationary centered green spot and, after 600–900 msec, a red target spot appeared 2° to the left or right of the fixation spot (initial target position) but the monkey had to continue fixating the green spot for at least another 300 msec. At this point, subsequent events depended on which block was being run: In Experiment 1a, the green spot was immediately extinguished, and the monkey was required to transfer fixation to the red spot, which either remained stationary (saccade trial) or started to move rightward or leftward at a constant speed of 20°/sec (pursuit trial) for 800 msec. In Experiment 1b, the green spot remained on and the red spot was moved briefly (perturbation: one cycle of a 10-Hz triangle wave, peak-to-peak amplitude = 1°, peak-to-peak velocity = 40°/sec, so that the motion for the first 50 msec was identical to the motion of the pursuit target in Experiment 1a), either start leftward or start rightward, after which the target remained stationary for a further 100 msec before starting to move with a motion that was identical to the above-described motion in the no-perturbation trials. The animal was required to make a saccade to the target when it was stationary or to track it when it moved. The initial target position, the direction of the perturbation, and the direction of the pursuit target motion were selected at random each trial. The ocular responses to perturbations initially directed away from the screen center (centripetal) were generally small compared with the responses to perturbations initially directed towards the screen center (centrifugal), as previously reported (Tabata et al., 2004). Therefore, we analyzed only the responses to initially centripetal perturbations (Experiment 1b) and motions (Experiment 1a). For half of the experiments, the TMP started with low and ended with high probability and for the remaining half, this order was reversed.

The latency of smooth pursuit onset was determined from the mean eye velocity profiles following our...
previous study (Miura, Suehiro, Yamamoto, Kodaka, & Kawano, 2001). First, we determined the mean eye velocity over a 100-msec interval beginning 50 msec before the onset of target motion (preresponse baseline) and computed the regression line of the preresponse baseline (line b). Then, we determined the earliest time (time, r) at which the response exceeded the preresponse baseline by 3SDs. We then computed the regression line over a 90-msec interval starting 10 msec before time r (line, r). Finally, we computed the time at which line r intersected with line b.

**Experiment 2**

The pictorial representation of Experiment 2 is shown in Figure 1C. In this experiment, we focused on the time course of changes in the ocular responses when the TMP was changed. The initial target position and the direction of the perturbation were fixed. At the beginning of each trial, the animal had to fixate the central green spot for 600–900 msec. Then a red target spot appeared 2° above the green fixation spot. The animal had to keep fixating on the green spot until it went off. Three hundred milliseconds after it appeared, the target was briefly moved horizontally (perturbation). The perturbation was one cycle of a 10-Hz sine wave with a peak-to-peak amplitude of 0.3° and a peak-to-peak velocity of 20°/sec. The direction of the velocity change was leftward start in all trials. After the end of the perturbation, the red spot stayed at the original position for 100 msec. Then the green fixation spot was turned off, and the red spot remained stationary or began to move at 20°/sec either leftward or rightward, selected at random in each trial. The animal was required to make a saccade to the target when it was stationary or to track it when it moved.

The task sequences consisted of successive subblocks, each subblock consisting of 50 trials as shown in Figure 1D. In each subblock, the target motion (either stationary or ramp motion) in a given trial was based on the TMP (0 for subblock 1, and 0.5 or 1 for subblock 2). We designed two types of subblock sequences. We assigned trial numbers 1 to 50 to subblock 1, and 51 to 100 to subblock 2. In Sequence 1, TMP = 0 subblocks alternated with TMP = 1 subblocks, and in Sequence 2, TMP = 0 subblocks alternated with TMP = 0.5 subblocks. A complete sequence involved 20 repetitions of each subblock. We removed the first subblock of the day from the analysis because our interest was in the transition of ocular responses due to the change in TMP. We calculated the magnitude of the perturbation responses from mean eye velocity in an 80-msec interval starting from 70 msec after the target motion onset.

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**REFERENCES**


